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TWO NEW SPECIES OF *MIMAGONIATES* (TELEOSTEI: CHARACIDAE: GLANDULOCAUDINAE), THEIR PHYLOGENY AND BIOGEOGRAPHY AND A KEY TO THE GLANDULOCAUDIN FISHES OF BRAZIL AND PARAGUAY

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Abstract.—Two new species of freshwater glandulocaudine characid fishes are described from coastal streams of eastern Brazil. The first, *Mimagoniates sylvicola,* is from southeastern Bahia, the second, *Mimagoniates rheocharis,* from southeastern Santa Catarina and northeastern Rio Grande do Sul. *Mimagoniates sylvicola* is hypothesized to form an unresolved trichotomy with *Mimagoniates lateralis* and a monophyletic line leading to the more derived *Mimagoniates microlepis* and *Mimagoniates rheocharis. Mimagoniates rheocharis* most parsimoniously appears to be a sister species of *M. microlepis* but its phylogenetic relationships may be quite complex and its possible introgression with *M. inequalis* and/or its origin by introgression between *M. inequalis* and *M. microlepis* is discussed. Solution to this problem awaits additional data based on more appropriate population samples than available to us and on genetic information. The biogeography of all these species is briefly discussed on the basis of the limited available phylogenetic information.

The descriptions of the new fish species herein continue a series of contributions to the knowledge of the fauna of the streams of the east coast of Brazil. As discussed by Weitzman et al. (1986:344–345), the freshwater fish fauna of the coastal or littoral streams of eastern Brazil appears to contain many new species, a fact unrecognized until the last 15 or 20 years. The descriptions provided here are a product of a continuing study by us of the Glandulocaudinae, a characid subfamily distributed from Costa Rica south to northern Argentina in Atlantic drainages and to the Guyas basin in Pacific drainages. We describe these new fishes here because we wish to have them available for a phylogenetic analysis of the Glandulocaudinae and especially the Glandulocaudini in progress.

The Glandulocaudini, one of apparently four tribes of the Glandulocaudinae (Weitzman et al. 1988:383, Weitzman et al. *in* Weitzman & Fink 1985:112–117), currently consists of two genera, *Glandulocauda* Eigenmann (1911) and *Mimagoniates* Regan (1907). Use of the generic names *Mimagoniates, Coelurichthys* Miranda-Ribeiro (1908) and *Glandulocauda* in the tribe has changed frequently, with little agreement among various authors. Weitzman & Fink (1985:1, 2, 109) reviewed some of the nomenclatural and phylogenetic problems regarding the generic names of the tribe. We follow their usage until ongoing studies allow us to evaluate the present preliminary phylogeny of the tribe based on more abundant data than shown in Fig. 1.

The Glandulocaudini contains eight known species, including the two described here. Schultz (1959), the last author to review the species of the Glandulocaudini in any detail, accepted five species. He considered *M. lateralis* (Nichols) a synonym of *M. inequalis* (Eigenmann). These two species

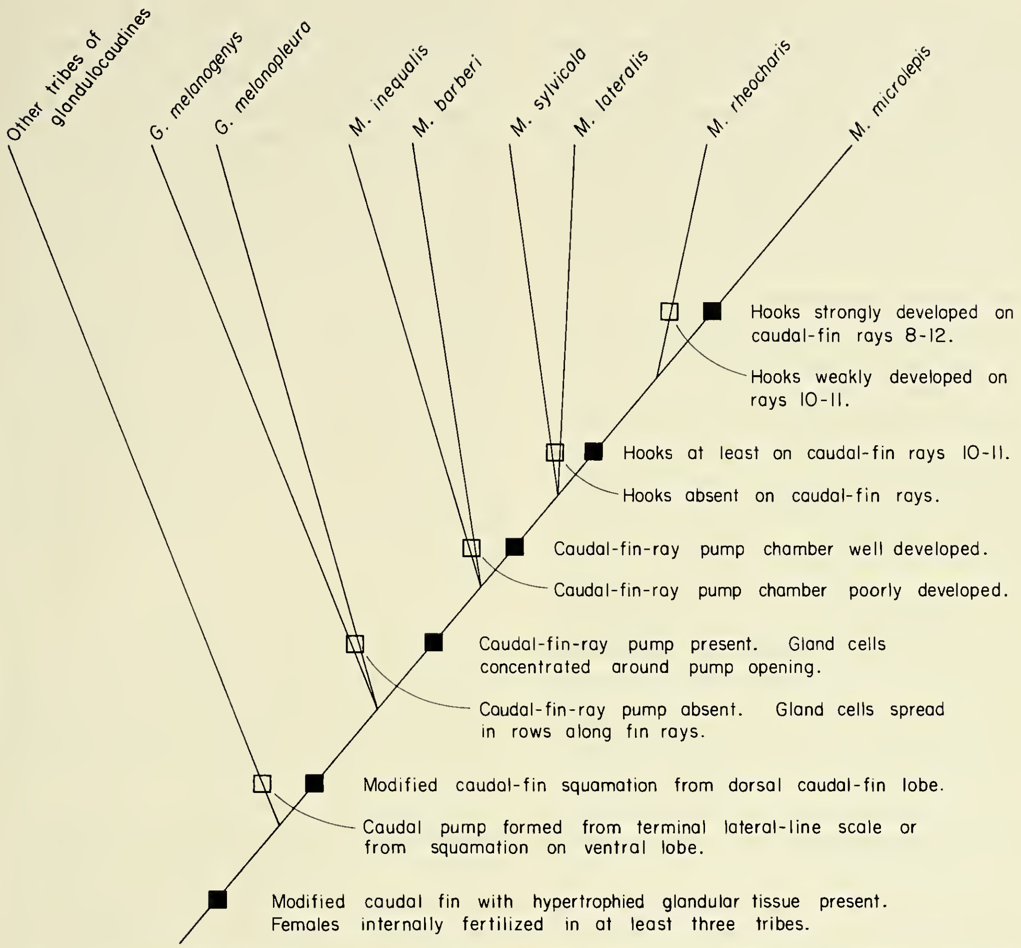

Fig. 1. Diagram of tentative phylogenetic relationships of the species of the Glandulocaudini based on an analysis of synapomorphies found in the caudal skeleton of males. Filled in squares = apomorphies and empty squares = plesiomorphies at the levels indicated.

are recognized as distinct and valid here. Géry (1966:228–230) constructed a key to the tribe and recognized seven species. He appeared doubtful that the group as presented by Schultz or himself was monophyletic. Six of the species tentatively included as valid by Géry are among those accepted here. Inclusion of Géry's seventh species, *Glandulocauda terofali* Géry (1964), would make polyphyletic the monophyletic Glandulocaudini as defined below. This species lacks the modified dorsal lobe caudal-fin squamation that is synapomorphic for the adults of both sexes of all species included by us in the Glandulocaudini. It also lacks the ventrally bowed form of caudal-fin rays 11 and 12 or the particular kind of modification into caudal fin-ray pump structures which form a synapomorphic morphological transformation series confined to members of this tribe. See the key below for a summary exposition of these glandulocaudin characters. We follow Weitzman & Fink (1985:103, 109) in assigning Géry's species to *Diapoma* Cope and accept *Diapoma terofali* (Géry) as a member of the glandulocaudine tribe Diapomini because it has the derived ventral lobe caudal-fin squamation in both sexes closely matching that of *Diapoma speculiferum* Cope. This squamation pattern (see Weitzman & Fink, 1985:fig. 15) is synapomorphic for the Diapomini, which also includes the species of *Acrobrycon* Eigenmann & Pearson and *Planaltina* Böhlke.

The keys to the species of the Glandulocaudini presented by Schultz (1959) and Géry (1966) were based on information from previous literature, some of the types and a few additional specimens. Because we are describing two new species and have examined all of the types and have new information from over 200 recently collected population samples, we provide an almost entirely new key to the species of the Glandulocaudini. See Weitzman et al. (1988:384–390, figs. 5, 6) for distribution maps and a summarized comparison of the collections available to Schultz and to us. A preliminary discussion of the Glandulocaudini, its phylogeny and biogeography were presented by Weitzman et al. (1988:384–419). See also Weitzman & Fink (1985:98–99) for a discussion of the morphology and possible function of the fin-ray pheromone pump mechanism of the species of *Mimagoniates*.

The two new species described below were designated as "new species A" (here = *M. sylvicola*) and "new species B" (here = *M. rheocharis*) in Weitzman et al. (1988). A third putative species, "new species C," recognized as possibly new by them, appears closely related to *M. microlepis* (Steindachner) and may be one of several relatively distinct populations of this species. The relationships among and distinctness of these populations is a complex problem and will require extensive analysis, research not undertaken here.

The importance of well-documented phylogenies to biogeographic hypotheses is emphasized by the changes noted below in the section on biogeography. A change in our tentative understanding of the phylogenetic relationships of *M. sylvicola* based on a population sample unavailable to Weitzman et al. (1988) resulted in a consequent change in our hypotheses regarding the biogeographic history of the species of *Mimagoniates*. Compare the tentative phylogenetic diagram presented here, Fig. 1, with that of Weitzman et al. (1988:fig. 10). The phylogenetic and biogeographic accounts by Weitzman et al. (1988:414–419) of *M. rheocharis* remain essentially unchanged, but questions are raised about of phylogenetic relationships of this species that could have extensive biogeographic consequences, depending on the nature of their answers. The phylogenetic relationships of all species of the Glandulocaudini need further investigation.

Methods and Materials

Counts and measurements are those described by Fink & Weitzman (1974:1–2). In the counts given in the text of the descriptions, the holotype is given first followed by the mean, range and number of paratypes counted given in parentheses. The posterior terminal ray of the dorsal fin is not divided to its base and is counted as one. However, the posterior terminal ray of the anal fin is so divided and thus the apparent two posteriormost rays of the anal fin are counted as one. Note that "branched rays" refers to all rays posterior to the anterior unbranched rays of a given fin even if, as with the posterior terminal ray of the dorsal and pectoral fins, the posterior rays are unbranched at their bases or their distal segments. Body depth was measured vertically (orthogonal to the longitudinal body axis) from the dorsal-fin origin. All measurements other than standard length (SL) are expressed as a percentage of SL except subunits of the head which are recorded as a percentage of head length. Total vertebral counts (including the Weberian apparatus) were taken from radiographs and from cleared Alizarin red and Alcian blue stained preparations. These preparations are called "cleared and stained" in the text. The terminal "half centrum," hypural bones and associated vertebral elements, usually designated as PU_1+U_1, but not necessarily consisting only of those elements (Schultze & Arratia 1989:203) was counted as one vertebral element.

Statistical comparisons and basic statistics of characters taken from population samples were computed using SYSTAT (version 4.0, Systat, Inc., 1989) and BIOM-PC (version 2, Exeter Publishing Ltd, 1988). All hypotheses of statistical significance are two-tailed. Common logarithms were used for transformations of original data used in covariance analyses. In the morphometric scatter plots, both axes are logarithmic and the regression lines are based on log transformed data plotted in the figures. Regression equations given in the figure captions are based on logarithmic transformations of original data and correspond to their respective logarithmic transformed covariance analyses in the text. The regression lines and equations are given only to present a concept of the comparative approximations of the growth lines of sexually maturing and mature population samples within the limits of the data. In no instances are regression lines, regression equations or covariance analyses to be construed as predictors of body shape beyond the data shown in the appropriate plots. Logarithmic regression lines and semilogarithmic scatter plots were prepared using Sigma-Plot (version 3.10, Jandel Scientific, 1988). In cases where a value of a *t*-statistic was computed for comparisons of population means of counts, square-root transformations were utilized. In the key, and abbreviated parts of the diagnoses, the ranges, means and other statistical parameters that may be given are for all of the paratypes and the holotype of each respective new species. In the statistical comparisons (statistical hypotheses of differences), ranges, means and other statistical parameters are naturally limited to the population samples being compared.

In our discussions, comments on phylogeny are based on the concepts of phylogenetic systematics of Hennig (1966) as reviewed and discussed by Wiley (1981). Maddison et al. (1984) are followed for outgroup considerations. Biogeographic principals follow Humphries & Parenti (1986).

Specimens examined for this study are deposited in the Museu Anchieta, Porto Alegre (MAPA), Museu de Zoologia da Universidade de São Paulo (MZUSP); the Smithsonian Institution, National Museum of Natural History (USNM); Museu de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul (MCP); Museum of Zoology, University of Michigan (UMMZ) and the California Academy of Sciences (CAS). Specimens examined in detail, other than those listed or cited here, were listed in Weitzman & Fink (1985:102–108.

Geographic entities (such as rivers) and place names (except those of countries) are in the language of the country of origin. Countries are in English because there is an English name for the various countries. Therefore rio (rio in Portuguese, río in Spanish) is not capitalized when referring to a river (thus rio Jordão and rio Grande), but it is capitalized when referring to a place name (thus Rio de Janeiro and Rio Grande do Sul). We do this because we are attempting to avoid the transferal of English style and grammar onto foreign localities and geographical units.

Key to the Species of the Glandulocaudini

Although this key employs many characters that are apparently synapomorphic at their level of use, the key is not a hypothesis of phylogeny for any of the included taxa except for the Glandulocaudini diagnosed in the first half (1a) of the first couplet. Because the primary purpose of this key is to identify species, we use any appropriate character that either clusters and/or distinguishes species. Thus, except for couplet 1a where the characters are synapomorphies, a given character may be either a plesiomorphy, a synapomorphy or an autapomorphy at its point of use. At this time we lack corroborated polarity hypotheses for many of the characters that are not associated with the secondary sexual features of adult males and our hypotheses for the secondary sexual characters cannot be considered well-supported. Homoplastic characters are used where they serve the purpose of the key. The reader should note that when using couplet 4, many maturing males of species of *Mimagoniates* that have a well-developed caudal pump chamber when fully mature, will key to 4a rather than 4b (where they belong) because of the incomplete development of the specimen's caudal fin-ray pump. This will often be the case in relatively small and some moderate sized specimens even in the presence of apparently active testes.

1a. Adult males and females with modified caudal-fin squamation extending posteriorly onto caudal fin from base of ventral portion of dorsal caudal-fin lobe; principal caudal-fin rays 11 and 12 of adult males somewhat bowed or curved ventrally, these and adjacent rays modified into a chamber or support for a chamber of a fin-ray pump organ in some species (compare Figs. 2–6) .... Glandulocaudini (2)

1b. Adult males and females without modified caudal-fin squamation or, if such scales present, then these derived from both caudal-fin lobes, only from ventral caudal-fin lobe or primarily from terminal lateral-line scale; principal caudal-fin rays 11 and 12 of adult males straight or if modified, not bowed ventrally (as in Fig. 6) or modified into a fin-ray pump organ (as in Figs. 2–5) although they may provide origins for muscular and ligamentous attachments to a scale-diaphragm pump mechanism .... other tetragonopterine or glandulocaudine characid groups

2a. Caudal fin-ray pump absent in all sexes at all ages (see Fig. 6); hypertrophied glandular tissue widespread along caudal-fin rays, especially those of ventral caudal-fin lobe, but most dense along proximal portions of rays 11 and 12; more than 1 hook on each anterior anal-fin ray that bears hooks .... *Glandulocauda* (3)

2b. Caudal fin-ray pump present in mature males, modified primarily from caudal-fin rays 10–12, sometimes relatively simple and represented by expanded, flattened anterior portions of ray halves, sometimes by an anterior fin-ray pump chamber; hypertrophied glandular tissue confined to area immediately around and on caudal pump region of gland (see Figs. 2, 5); no more than 1 hook on any anal-fin ray that bears hooks .... *Mimagoniates* (4)

3a. Branched anal-fin rays 20–23; perforated lateral line scales 11–21; scale rows between dorsal-fin origin and anal-fin origin 14–17; scale rows around caudal peduncle 17–18, usually 18; dorsal-fin origin somewhat anterior to vertical line drawn from anal-fin origin ....*Glandulocauda melanogenys* Eigenmann (upper rio Tietê, in São Paulo, Brazil)

3b. Branched anal-fin rays 15–18; perforated lateral-line scales 4–6; scale rows between dorsal-fin origin and anal-fin origin 11–13; scale rows around caudal peduncle 16; dorsal-fin origin somewhat posterior to vertical line drawn from anal-fin origin .... *Glandulocauda melanopleura* Eigenmann

(upper rio Iguaçu, in Paraná and Santa Catarina, Brazil)

4a. Caudal fin-ray pump little developed in males of completed sexual maturity and without obvious pump chamber enclosed by modified proximal portions of caudal-fin ray halves 11 and 12; ray halves of this region of these rays modified into expanded, flattened structures parallel to one another; these modified ray halves of each side of caudal fin developed so that a groove exists between them; groove and accompanying hypertrophied glandular tissue constitute a primitive pump organ (see Figs. 2, 3) (5)

4b. Caudal fin-ray pump well-developed in males of completed sexual maturity, consisting of bilateral chambers, one on each side of fin and each chamber enclosed by flattened expanded portions of ray halves of rays 11 and 12; pump chamber with an obvious posterior opening, lateral slit and anterior opening (see Figs. 4, 5) .... (6)

5. Branched anal-fin rays 23–29, usually 25–27, rarely 28 or 29; scales in lateral series (including lateral line scales) 36–41, usually 37–40; scale rows between dorsal-fin origin and anal-fin origin 16–18; dorsal-fin origin at vertical line drawn from base of second or third branched anal-fin ray; mid-lateral dark body stripe of adult males diffuse, poorly developed, often not apparent; body depth approximately 2.7 to 3.3 in SL .... *Mimagoniates inequalis* (Eigenmann)
dos Patos and lagoa Mirim, in Rio Grande do Sul, Brazil and northeastern Uruguay)

5b. Branched anal-fin rays 30–36; scales in lateral series 41–48; scale rows between dorsal-fin origin and anal-fin origin 13–15; dorsal-fin origin at line drawn vertically from base of seventh to ninth branched anal-fin rays; lateral dark body stripe of adult males nearly black, clearly distinct; body depth at dorsal-fin origin about 4.0 to 4.5 times in SL . . . *Mimagoniates barberi* Regan
(tributaries of rio Paraguay in parts of Brazil and Paraguay)

6a. Hooks absent on all principal caudal-fin rays of adult males (see Figs. 3, 11, 12) .... (7)

6b. Hooks present on at least principal caudal-fin rays 10 and 11 of adult males, hooks also frequently present on ray 12 (see Figs. 5, 21) . . . (8)

7a. Lateral series scales 49–56; scale rows between dorsal-fin and anal-fin origins 16–18; body depth of adult males 3.4–3.8 in SL; in wild caught specimens body silvery blue, when black horizontal stripe present, located at and partly dorsal to mid-lateral region of body from tip of snout to central caudal-fin rays, stripe diffuse and broad and often obscured by silvery blue coloration posteriorly and by silvery pigment anteriorly; stripe rarely clearly defined .... *M. sylvicola,* new species
(tributaries of Atlantic Ocean in southern Bahia, Brazil)

7b. Lateral series scales 37–44; scale rows between dorsal-fin and anal-fin origins 12–15; body depth of adult males 3.8–5.1 in SL; in wild caught specimens body mahogany brown, especially dorsally, with dark brown, nearly black, horizontal lateral body stripe below mid-region of body prominent and extending from tip of lower jaw, posteriorly ventral to eye, across opercle and body sides just ventral to mid body region onto caudal peduncle and across central portion

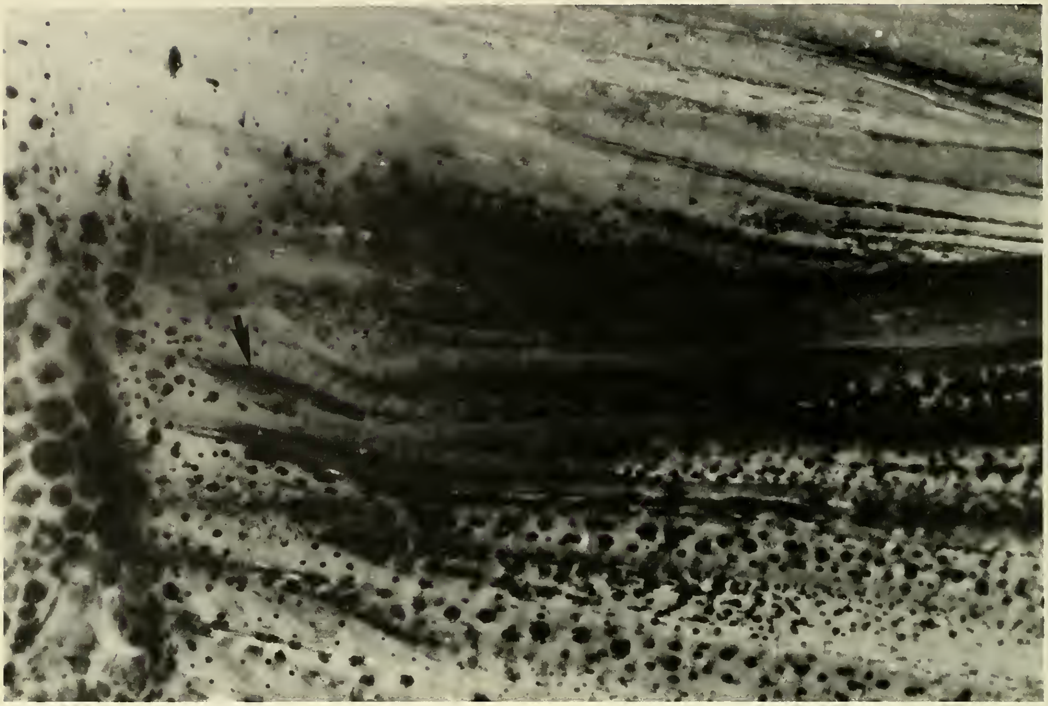

Fig. 2. *Mimagoniates barberi,* unstained central basal region of caudal fin adjacent to caudal peduncle of a preserved adult male, lateral view, left side, anterior at left. SL 32.7 mm, UMMZ 205420, Paraguay, río Aguarymi, tributary to río Paraguay, San Pedro. Illustrates external features of a caudal gland without complex pump chamber. Darkly pigmented glandular groove between principal rays 11 and 12 indicated by arrow. Modified dorsal caudal-fin lobe scales, although present, are transparent and not visible.

of caudal fin ....
.... *Mimagoniates lateralis* (Nichols)
(tributaries of Atlantic Ocean from Santos, São Paulo south to Joinville, Santa Catarina, Brazil)

8a. Branched anal-fin rays 23–29, usually 24–26; branched dorsal-fin rays 8–12, rarely 8; scale rows between dorsal-fin origin and anal-fin origin 17–22, usually 19–20; scale rows around caudal peduncle 19–23, usually 20–22; branched dorsal-fin rays 8–12, rarely 8; very small hooks on caudal-fin rays 11–12 of fully adult males (Fig. 21); dorsal-fin origin at vertical line drawn from anal-fin origin or from base of 2 to 4 rays posterior to anal-fin origin ....
...... *Mimagoniates rheocharis,* new species
(tributaries to Atlantic Ocean of southern Santa Catarina and northern Rio Grande do Sul, Brazil)

8b. Branched anal-fin rays 26–33, usually 28–31; branched dorsal-fin rays 7–9, rarely 9; scale rows between dorsal-fin origin and anal-fin origin 14–17, usually 15–16; scale rows around caudal peduncle 15–18; numerous strong hooks on at least caudal-fin rays 11–12 (sometimes 7–12) of fully adult males (see Fig. 5); dorsal-fin origin at a vertical line drawn from base of branched anal-fin rays 5 or 6 .
.... *Mimagoniates microlepis* (Steindachner) (tributaries to

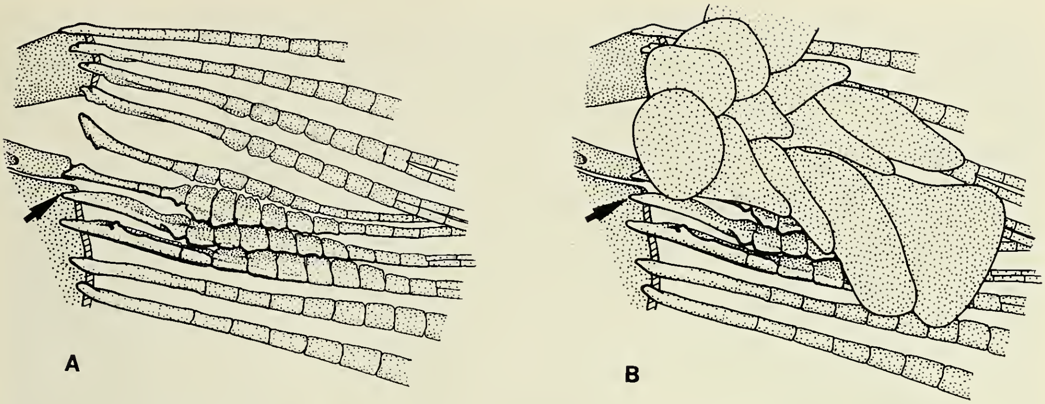

Fig. 3. *Mimagoniates barberi,* osteology of central basal region of caudal-fin skeleton, principal fin-rays 6–15, of adult male, lateral views, left side, anterior at left. SL 35.6 mm, UMMZ 205420, same locality as Fig. 2. Principal ray 12 indicated by arrow. (A) Illustrates glandular groove between rays 11 and 12. (B) Illustrates relationship of modified dorsal caudal-fin lobe squamation to glandular groove. Note that modified scales together with their epidermis form a movable flap just lateral to surface of rays and glandular groove. Free border of this flap occurs along ventral margin of ventral row of scales and at posterior edge of posterior scale of ventral scale row.

Atlantic Ocean from southern Bahia south to northern Rio Grande do Sul, also in upper rio Iguaçu, Paraná)

Mimagoniates sylvicola, new species
Figs. 7–16, Table 1

Species A.—Weitzman et al., 1988:figs. 6, 10 [phylogeny and biogeography].

Holotype.—MZUSP 36612, male, SL 30.2 mm, Brazil, Bahia, Município de Prado, forest stream tributary to Atlantic Ocean, near Fazenda Embaçuaba, approximately 8–9 km NW of Cumuruxatiba, 17°05′S, 39°13′W, 20 Mar 1985; N. Menezes, R. M. C. Castro, M. Weitzman, and S. Weitzman.

Paratypes.—Following 2 lots of immatures to adults collected with holotype: MZUSP 28817, spms. 42, SL 15.1–30.2 mm; USNM 276557, spms. 42, SL 14.7–33.5 mm, 1 male SL 29.3 mm and 1 female SL 26.6 mm [both cleared and stained]. Following lots of immature to adult paratypes all collected 20 Mar 1985 by N. Menezes and party unless otherwise noted: MZUSP 28815, spms. 77, SL 11.0–27.4 mm; USNM 276547, spms. 77, SL 14.4–27.4 mm, Brazil, Bahia, Município de Prado, first stream (locally called rio do Sul) south of rio Caí, on road between Cumuruxatiba and Itamaraju, 17°00′S, 39°12′W. MZUSP 28816, spms. 28, SL 12.7–25.1 mm; 6, spms. 25, SL 13.2–24.0 mm, Brazil, Bahia, Município de Prado, small stream NW of Cumuruxatiba, about 17°01′S, 39°12′W. USNM 300633, spms. 5, SL 22.3–31.3 mm and USNM 300634, spm. 1, cleared and stained, SL 31.8 mm, Brazil, Bahia, Município de Porto Seguro, riacho Ronca Água, tributary to right margin of rio Camurugi, tributary to rio João de Tiba drainage, 15 km NW of Porto Seguro, approximately 16°20′S, 30°07′W, 19 Feb 1986, I. Rosa and party.

Diagnosis.—*Mimagoniates sylvicola* may be separated from all other species of *Mimagoniates* by use of the key to the species provided above. It is distinguished from its morphologically most similar relative, *M. lateralis,* by the following characters: lateral series scales 49–56 (37–44 for *M. lateralis*), scale rows between dorsal-fin and anal-fin origins 16–18 (12–15 for *M. lateralis*). Certain body measurement ratios differ signif-

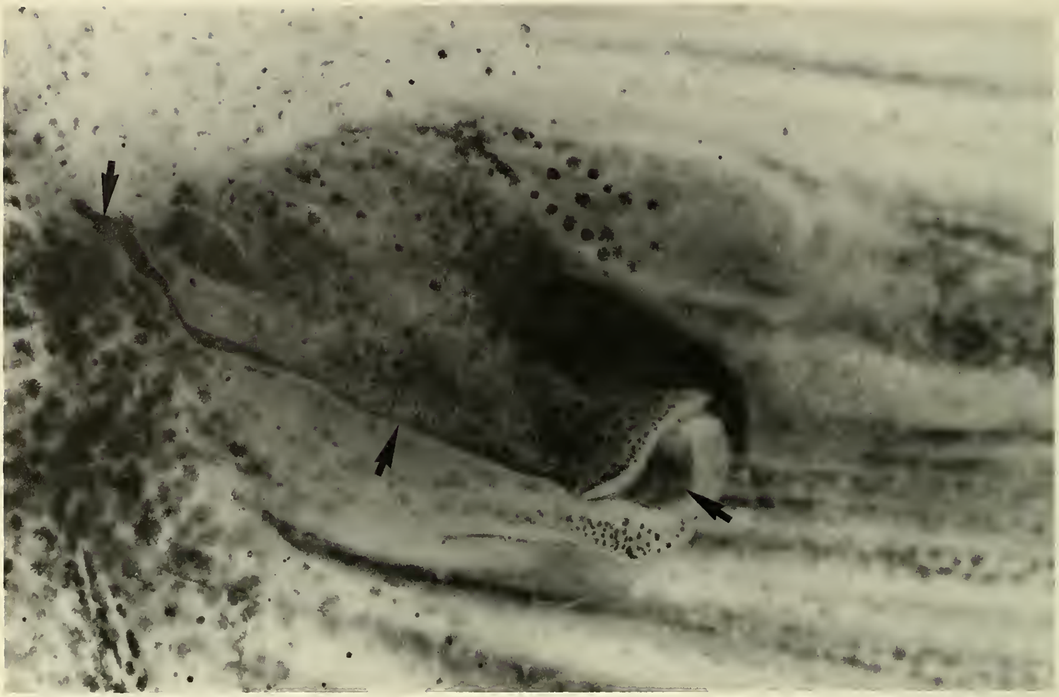

Fig. 4. *Mimagoniates microlepis,* unstained central basal region of caudal fin adjacent to caudal peduncle of a preserved adult male, lateral view, left side, anterior at left. SL 51.7 mm, USNM 279876, Brazil, Santa Catarina, rio Itapocú. Illustrates external features of a caudal gland with a complex pump chamber. Arrow at left indicates anterior intake opening, middle arrow indicates lateral slit of chamber and arrow at right designates posterior exit opening of chamber. These openings surrounded by glandular tissue, especially exit opening. Modified dorsal caudal-fin scales appear as rather poorly focused "ghost" images in upper half of picture, above main body of pump chamber.

icantly between adults of these species but overlap broadly in young and juveniles. For example, body depths in adult males and females of *M. sylvicola* diverge considerably from those in adult males and females of *M. lateralis* (body more elongate and slender). See "*Discussion*" below and Figs. 15, 16. Preserved and live colors differ between the species. Preserved males of *M. sylvicola* with dark lateral body stripe relatively pale and diffuse, occurring mostly at and partly dorsal to mid-lateral body region. Approximately dorsal half of opercle dark, nearly black (relatively pale in *M. lateralis*). *Mimagoniates lateralis* with a dark, relatively narrow, clearly defined lateral body stripe that lies mostly ventral to mid-lateral body region. Dark stripe continues onto ventral one-third of opercle. Males of *M. sylvicola* with distal one-fourth to one-fifth (less posteriorly) of anal-fin rays black (distal two-thirds to one-half black in *M. lateralis*). Males of *M. lateralis* with distal one-fourth of most elongate anterior unbranched ray and branched portions of anterior five to six branched rays hyaline or with a thin scattering of dark chromatophores, never black as in *M. sylvicola.* Numerous other, but less obvious, color differences occur in preserved males of both species. These best discerned by comparing respective color descriptions given below. Life color of these

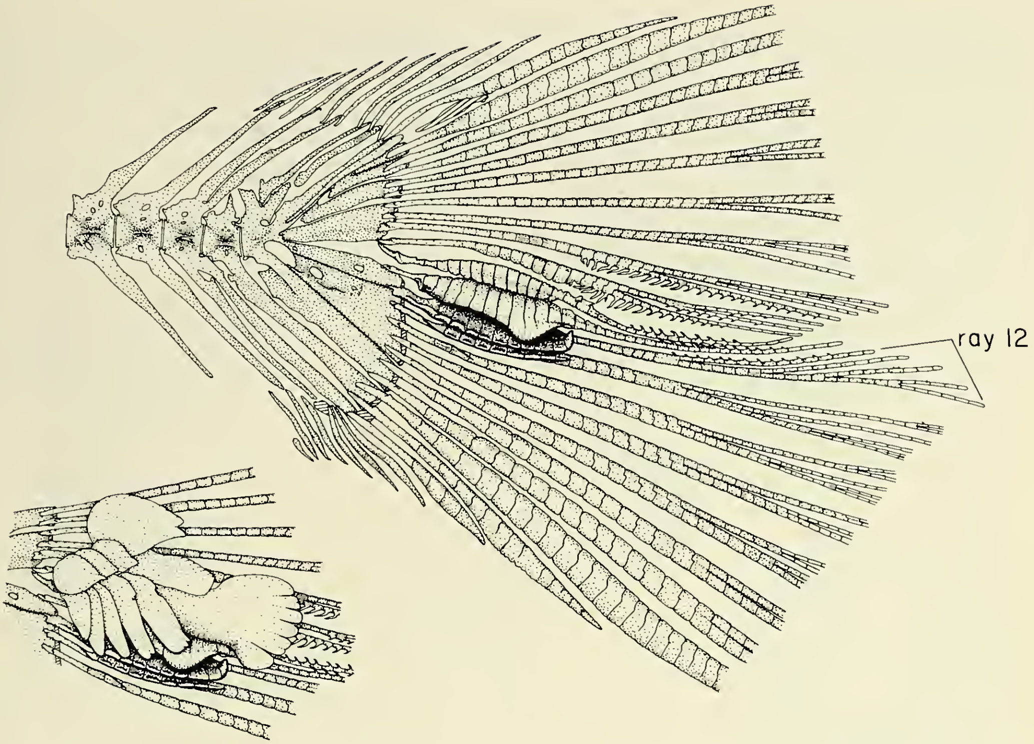

Fig. 5. *Mimagoniates microlepis,* osteology of central and basal region of caudal skeleton of adult male, lateral view, left side, anterior at left. SL 45.3 mm, USNM 236089, Brazil, Paraná, rio Nhundiaquara at Morretes. Relationship of modified dorsal lobe caudal-fin squamation to caudal gland shown in inset at left. Distal regions of ventral and posterior scales and their epidermis form a flap partly covering intake openings of pump chamber.

species quite different. Male *M. sylvicola* with dorsally located black lateral "stripe" obscured by silvery blue reflective color, especially anteriorly. Ventrally located black stripe of male *M. lateralis* deep black except at its mid-length ventral to dorsal-fin origin where partly obscured by blue to silvery pigment in some population samples. Wild caught males of *M. lateralis* with a yellow-orange stripe just ventral to black lateral stripe, absent in *M. sylvicola,* although both species often with anal-fin base yellow to orange. Note, in aquaria at least, *M. lateralis* loses yellow or orange coloration but black stripe always present. See live color descriptions below for a more complete account of *M. sylvicola.*

Description.—Table 1 presents morphometrics of holotype and paratypes. Except where noted, entire description refers to lots from near Cumuruxatiba. These collections are treated statistically as one population sample since no statistical differences were found among them and all lots were collected from only a few kilometers apart. Counts for specimens from rio Camurugi are given only when they differ from those from near Cumuruxatiba.

Body compressed, moderately elongate; body deepest about midway between snout tip and dorsal-fin origin, near anal-fin origin. Predorsal body profile gently convex to snout tip. Body profile slightly elevated at dorsal-fin origin, straight along dorsal-fin base and nearly straight to origin of dorsal procurrent caudal-fin rays. Dorsal-fin origin

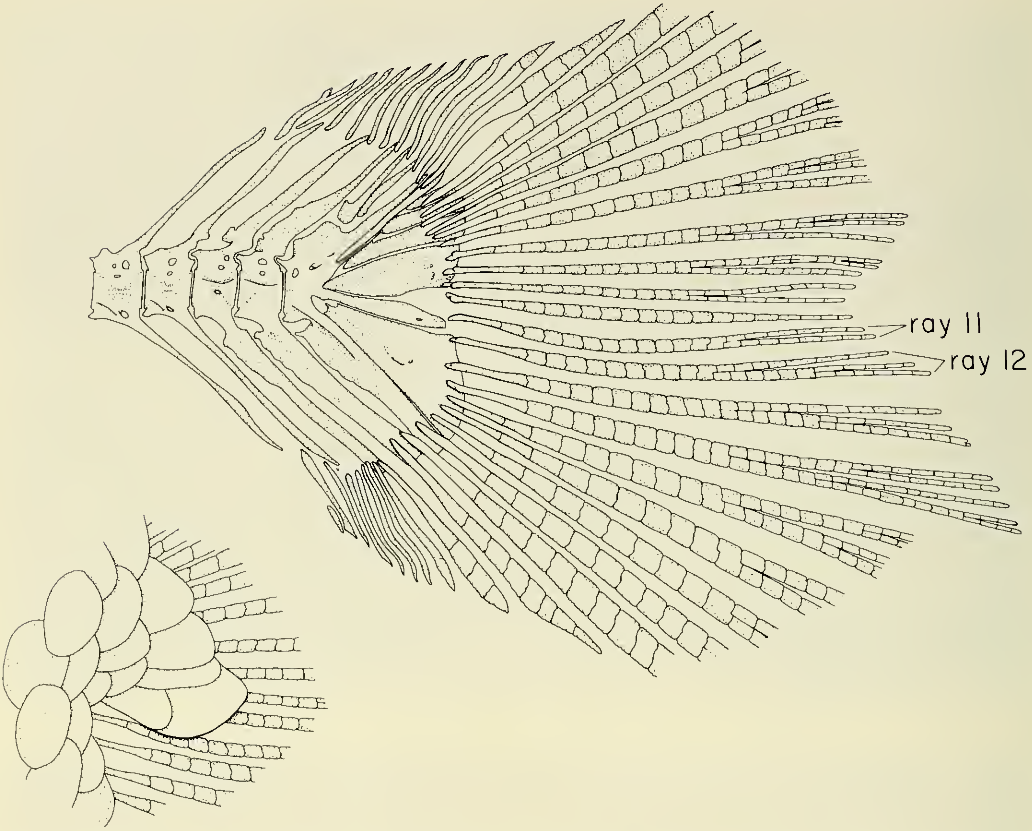

Fig. 6. *Glandulocauda melanogenys,* osteology of central and basal region of caudal skeleton of adult male, lateral view, left side, anterior at left. SL 40.2 mm, USNM 236093, Brazil, São Paulo, headwater stream of rio Tietê near Campo Grande (=Alto da Serra, type locality), about 3.5 km west of Paranapiacaba. Decurved principal caudal-fin rays 11 and 12 are labeled and inset at left illustrates relationship of modified dorsal caudal-fin squamation to rays 11 and 12. Note that modified caudal-fin squamation of females of in all species of *Glandulocauda* and *Mimagoniates* is very similar to that illustrated here but may reach only about half the relative dimensions depicted here.

nearer to caudal-fin base than to snout tip. Ventral body profile convex from anterior tip of lower jaw to point on abdomen about midway between pectoral- and pelvic-fin bases. Belly profile abruptly becomes concave and then straight to anal-fin origin. Body profile slightly convex along anal-fin base to anal-fin insertion. Ventral profile of caudal peduncle slightly convex, especially in adult males where profile formed by ventral procurrent caudal fin rays. In females and juveniles this profile nearly straight.

Head and snout of moderate size in proportion to body length. Lower jaw protruding, anterior to upper jaw. Lower jaw of males thick and heavy compared to that of females. Mouth angled posteroventrally from anterior tip of snout to posterior part of mandibular joint. Maxilla extending posteriorly to a point anterior of a vertical line drawn through anterior border of pupil of eye.

Dorsal-fin rays ii,8 (unbranched rays ii in all specimens, branched rays $\bar{x} = 8.0$ [3 spms. with 9], range = 8–9, $n = 90$); of 6 specimens from rio Camurugi (not included in $n = 90$)

Table 1. Morphometrics of *Mimagoniates sylvicola,* new species. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Specimens are from the area near Cumuruxatiba, Bahia, MZUSP 28815, 28816, 28817, 36612 and USNM 276547, 276556, 276557.

	Holotype	n	Range	$\bar{x}$
Standard length	30.2	88	14.5–30.2	20.9
Depth at dorsal-fin origin	—	88	20.7–29.3	24.9
Males	29.1	44	21.5–29.3	25.7
Females	—	44	20.7–27.2	24.0
Snout to dorsal-fin origin	61.6	88	57.1–63.8	60.1
Snout to pectoral-fin origin	28.1	88	24.3–29.0	26.3
Snout to pelvic-fin origin	43.4	88	39.8–46.9	43.3
Snout to anal-fin origin	55.6	88	54.4–61.0	57.1
Caudal peduncle depth	—	88	8.5–14.3	10.8
Males	13.2	44	8.7–14.3	11.6
Females	—	44	8.5–11.7	10.1
Caudal peduncle length	12.3	88	10.2–13.8	12.1
Pectoral-fin length	23.2	88	20.2–24.8	22.6
Pelvic-fin length	14.9	88	11.1–16.1	13.3
Dorsal-fin base length	14.2	88	11.8–16.6	13.8
Dorsal-fin height	19.2	88	14.4–21.0	18.1
Anal-fin base length	33.4	84	29.7–35.2	32.6
Anal-fin lobe length	19.2	87	17.2–22.6	20.1
Eye to dorsal-fin origin	46.4	88	42.9–51.0	46.3
Dorsal-fin origin to caudal-fin base	43.7	88	39.4–46.9	42.4
Bony head length	27.8	88	24.8–28.6	26.3
Horizontal eye diameter	35.7	90	33.7–47.4	40.6
Snout length	22.6	90	20.8–26.5	23.8
Least interorbital width	33.3	90	31.6–40.5	35.3
Upper jaw length	45.2	90	34.4–49.3	45.7

2 with 8 and 4 with 7 branched rays; posterior ray not split to its base and counted as 1. Adipose fin present, slender. Anal-fin rays iv,25 (unbranched rays iv in all specimens, branched rays $\bar{x}$ = 24.8, range = 23–26, n = 90); posterior ray split to its base and counted as 1. Anal fin with moderately developed lobed anterior portion including fourth unbranched ray and first 5–6 branched rays. Anal fin of sexually mature males with bilateral blunt hooks on anterior 6 branched fin rays, 1 set of hooks for each ray (see Fig. 9). Pectoral-fin rays i,10 (unbranched rays i in all specimens, branched rays $\bar{x}$ = 9.7, range = 9–11, n = 90); all 6 specimens from rio Camurugi with 10 branched rays. Posterior tips of longest pectoral-fin ray extend posteriorly beyond origin of pelvic fin; of about equal length in both sexes. Pectoral-fin rays without hooks. Pelvic-fin rays 8 (8 in all specimens except 1 with 9, n = 90). Pelvic fin with anterior most ray branched in all specimens (see Fig. 10). Adult males with total of over 100 small to tiny hooks present on rays of pelvic fin, distributed as in Fig. 10. Each ray bears 9 to over 40 hooks, depending on the maturity of the specimen and/or the fin ray examined.

Principal caudal-fin ray count 10/9 in all specimens (n = 90). Fin rays modified in association with caudal pheromone pump as in Figs. 11 and 12. Fig. 11 illustrates a relatively immature pump, while Fig. 12 shows a presumably mature pump in which pump chamber has well-developed water

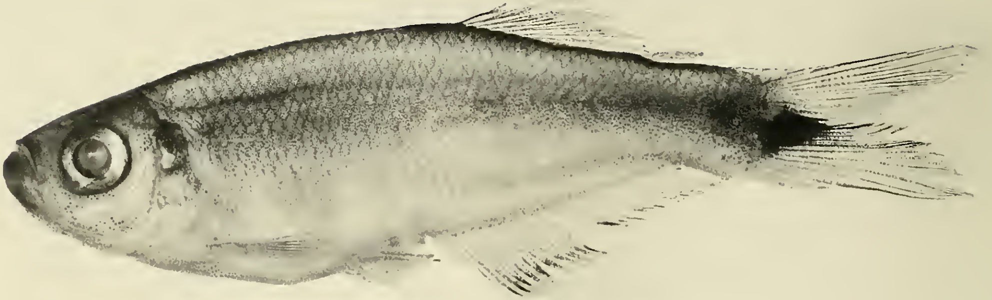

Fig. 7. *Mimagoniates sylvicola,* new species, holotype, MZUSP 36612, male, SL 30.2 mm; Brazil, Bahia, Município de Prado, unnamed forest rivulet near Fazenda Embaçuaba, 8–9 km northwest of Cumuruxatiba.

entrances and exit. Fin rays modified very much like those of *M. lateralis.* Caudal-fin rays without bony hooks. See also Weitzman & Fink (1985:98–99), Weitzman et al. (1988:384–413) and "*Discussion*" below, regarding phylogeny of *M. sylvicola* for hypothetical function of secondary sexual characters and phylogeny for glandulocaudins as indicated by their caudal pump morphology.

Scales cycloid, almost deciduous, with few radii along posterior border; smallest scales often nearly without or without radii. Terminal scale of modified caudal series with exaggerated radii appearing as incisions of posterior scale borders (see Figs. 11b, 12b).

Lateral line incomplete, perforated scales 8 ($\bar{x} = 7$, range = 6–8, $n = 34$); 2 specimens from rio Camurugi with 9 perforated scales. Lateral series scales 53 ($\bar{x} = 52.7$, range = 49–56, $n = 34$). Predorsal scales 25 ($\bar{x} = 25.9$, range = 24–28, $n = 39$). Scale rows between dorsal-fin origin and anal-fin origin 17 ($\bar{x} = 16.7$, range = 16–18, $n = 64$). Scale rows around caudal peduncle 20 ($\bar{x} = 19.7$, range = 19–20, $n = 21$); 1 specimen from rio Camurugi with 22 scale rows around caudal peduncle.

Premaxillary teeth in 2 distinct rows although this is not clear in Fig. 13. Larger teeth tricuspid, smaller teeth tricuspid or bicuspid, smallest ones unicuspid. Outer row teeth 6 ($\bar{x} = 5.4$, range = 3–7, $n = 90$). Inner row teeth 3 ($\bar{x} = 3.0$, range 2–5, $n = 90$). Outer and inner row premaxillary teeth somewhat compressed compared to most "tetragonopterine" characid teeth which often appear almost circular in cross section. Maxillary teeth 6 ($\bar{x} = 6.8$, range = 5–10, larger specimens usually with highest counts, $n = 90$); two specimens from rio Camurugi with 11 maxillary teeth. Maxillary teeth show an increase in number with increasing SL from a mean of 5.9 in 9 specimens between 15.5 and 16.5 mm SL to a mean of 7.6 in 14 specimens between 25.0 and 30.5 mm SL. Anterior 4–5 maxillary teeth tricuspid and larger than remaining teeth with 2 or 1 cusps. Dentary with 4 large tricuspid teeth in all specimens, $n = 90$; smaller posterior dentary series unicuspid except anterior tooth which is tricuspid, 10 ($\bar{x} = 8.9$, range = 6–12, $n = 90$); 1 specimen from rio Camurugi had 13 dentary teeth. Maxillary and dentary teeth shaped much like premaxillary teeth as described above. At any given SL considerable variation in tooth count occurs and nearly any tooth count within ranges given may be expected. No significant differences in tooth number found between males and females.

Vertebrae 40 ($\bar{x} = 39.9$, range = 39–41,

Fig. 8. *Mimagoniates sylvicola,* new species, paratype, USNM 276547, female, SL 25.7 mm, Brazil, Bahia, Município de Prado, rio do Sul.

$n = 88$). Dorsal limb gill-rakers 6 ($\bar{x} = 6.0$, range 6–7, $n = 90$, two specimens from rio Camurugi with 5 dorsal limb gill-rakers); ventral limb gill-rakers 12 ($\bar{x} = 11.7$, range = 11–13, $n = 90$). Branchiostegal rays 4 in 3 cleared and stained specimens, 3 rays originating from anterior ceratohyal and 1 ray from posterior ceratohyal.

Color in alcohol.—See Figs. 7 and 8 for preserved color pattern in males and females. Body pale to medium brown, almost white ventrally, darkest dorsally. Lateral body stripe pale, diffuse, best developed in males. Stripe extending from darker opercular spot on dorsal half of opercle posteriorly to a dark, spot-like region on caudal peduncle. Immediately posterior to this spot, caudal gland region enveloped in black pigment forming triangular-shaped area with its posterior apex continuous onto ray 11 and to a certain extent ray 12. Remainder of caudal fin dusky due to scattering of dark chromatophores, especially along ventral border of 19th principal caudal ray. Dorsal body surface dark dusky, especially in area of predorsal scales.

Pectoral, pelvic, dorsal and anal fins dusky from scattered dark chromatophores along fin rays. Pelvic fins considerably darker than pectoral fins. Anal fin with a dark, elongate stripe running length of fin. Width of stripe about ¼–⅕ height of fin. Stripe borders distal ends of fin rays posteriorly; anterior portion of dark stripe separated from distal ends of first five or six fin rays by relatively hyaline area on anterior lobe of fin. Dorsal fin with horizontal dark stripe extending posteriorly from about mid-length of anterior elongate undivided ray to posterior tips of two terminal dorsal-fin rays. Adipose fin dusky with scattered dark chromatophores. Head dark brown around mouth and on dorsal surface of snout, between eyes, dorsum of cranium and nape. Iris dorsal to pupil dark brown to black, most of remainder of iris silvery with some dark brown or black areas ventrally. Circumorbitals pale brown or silvery with evenly scattered dark chromatophores. Ventral area of opercle, preopercle and posterior region of branchiostegal rays silvery, without much dark brown pigment.

Color in life.—Life color patterns taken from color slides and color notes made while collecting specimens listed above from clear and black waters near Cumuruxatiba. Sides of body silvery deep blue with back dark brown and abdominal area silvery white. All fins translucent, lemon yellow with dark brown pigment described above under preserved color description appearing brown to black. Females with similar color pattern

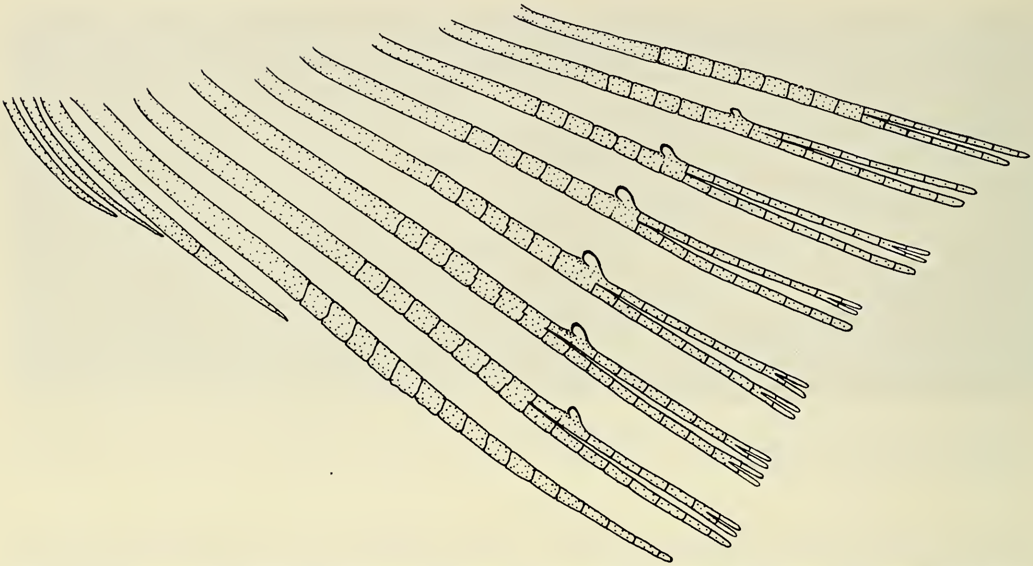

Fig. 9. *Mimagoniates sylvicola,* new species, paratype, anterior 11 anal-fin rays of an adult male, lateral view, left side, anterior at left, Sl 32.5 mm, USNM 300634, Brazil, Bahia, riacho Ronca Áqua. For explanation see Description of *M. sylvicola.*

but blue, yellow, and dark pigment patterns much paler. In life caudal-fin rays 13 and 14 considerably darkened with black pigment. Some male specimens display a considerable but rather diffuse lateral dark brown stripe below lateral mid-region of body, suggesting elongate lateral stripe of *M. lateralis.* Specimens from rio do Sul, Cumuruxatiba area (USNM 276547), gold silvery in color and without blue coloration. Some of these specimens with black pigment considerably reduced, absent or covered in patches by guanine, especially on body sides. These specimens may have been infested by metacercaria of a trematode as noted for other similar appearing characids by Géry & Delage (1963).

Sexual dimorphism.—Females lack the caudal pheromone pump organ, anal-fin and pelvic-fin hooks of males (Figs. 9, 10) and display a more subdued live body coloration as noted above. Figure 14 presents graphic evidence that the caudal peduncle depth is usually deeper in adult males than in adult females and that males reach a greater adult length than females, so far as known. Below in covariance analyses we compare males and females of unequal length ranges, although the range of the females is included within that of the males. We do this because we believe these ranges are expressions of their natural differences. In our population samples of various species of *Mimagoniates* the length of the largest males always exceeds that of the largest females. If in nature the females reached the same lengths as the males our results could be biased, but longer females were not represented in our samples. We hypothesize that most of our samples fairly represent the adult lengths of both sexes. Figure 14 indicates that caudal peduncle depth divergence between males and females begins around 18 mm in SL. Even though we have few female specimens in the size range between 23.0 to nearly 28.0 or longer, we are inclined to accept that 28.0 mm SL may be the approximate adult size limit for females. Also, at least some glandulocaudine species undergo delayed sexual maturation in males,

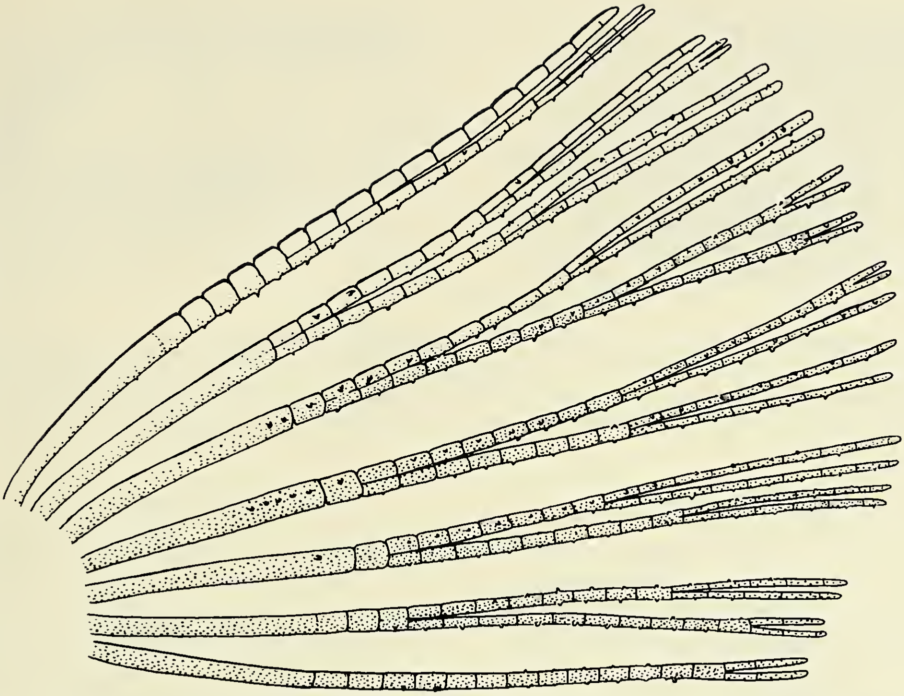

Fig. 10. *Mimagoniates sylvicola,* new species, paratype, pelvic-fin osteology of an adult male, ventral view, left side, anterior at left. SL 29.3 mm, USNM 276557, same locality data as holotype, Fig. 7. Medial fin-ray at bottom of picture.

Weitzman & Fink (1985:38, 42). If present in species of *Mimagoniates,* this kind of growth pattern might affect the regression slope shown for sexually maturing and sexually mature males towards that of the females in Fig. 14, if the large males of latent sexual maturity were included in the male population sample graphed and analyzed.

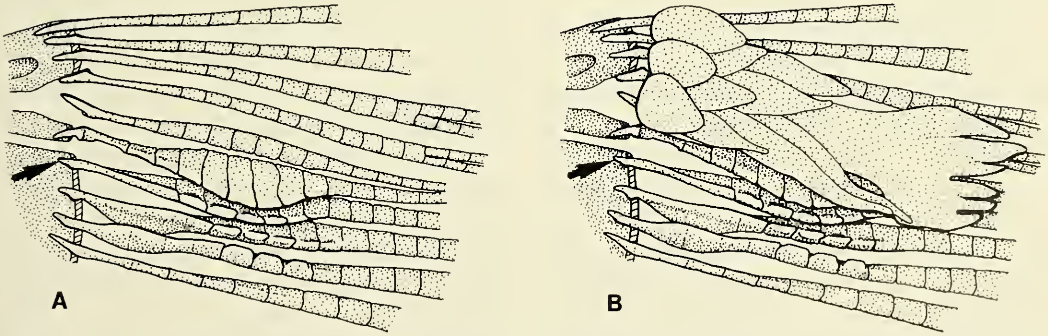

Fig. 11. *Mimagoniates sylvicola,* new species, paratype, osteology of central basal region of caudal-fin skeleton, principal rays 6–15, of an adult but still developing male, lateral views, left side, anterior at left. SL 29.3 mm, USNM 276557, same locality data as holotype, Fig. 7. Principal ray 12 indicated by arrow. (A) Illustrates area of developing rays associated with caudal pump. Note that pump chamber not yet fully developed. (B) Illustrates modified dorsal caudal-fin lobe squamation in natural position.

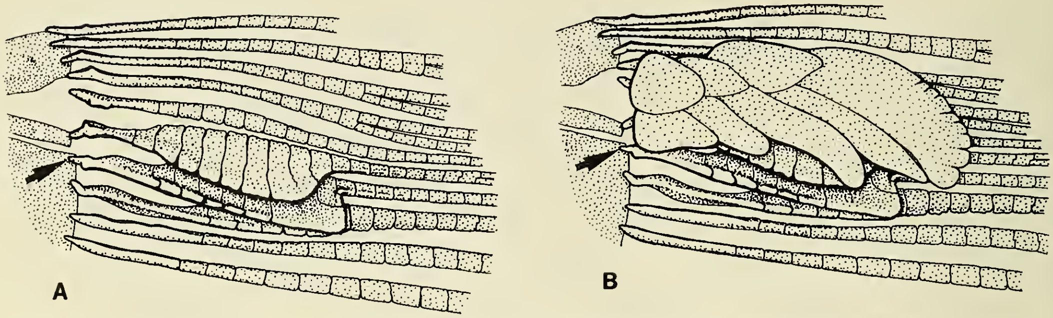

Fig. 12. *Mimagoniates sylvicola,* new species, paratype, osteology of central basal region of caudal-fin skeleton, principal rays 6–15, of an adult male, lateral views, left side, anterior at left. SL 32.5 mm, USNM 300634, Brazil, Bahia, riacho Ronca Áqua. Principal ray 12 indicated by arrow. (A) Illustrates area of fully developed caudal pump. (B) Illustrates relationship of modified dorsal caudal-fin lobe squamation to pump skeleton.

In the two slopes plotted in Fig. 14, latent males, if present, are included in that of the females. Thus Fig. 14 appears to demonstrate that as males mature sexually their caudal peduncles increase in depth at a faster rate relative to body length than it does in juveniles or females. With the above reservations and explanations in mind, we find that divergence in caudal peduncle depth on SL by apparent sex in an *F*-ratio test for homogeneity of slopes in an analysis of covariance were significantly different ($F_{0.05,(1,86)} = 9.42$, $P < 0.002$) between 45 males and 45 females from the area near Cumuruxatiba (MZUSP 28815, 28816, 28817, 36612 and USNM 276547, 276556, 276557).

Etymology.—The name *sylvicola* is from the Latin *silva* (forest) and *colo* (dwell or inhabit) and is in reference to the forested nature of the streams in which this fish is found.

Discussion.—Weitzman et al. (1988:404, 414–419, fig. 10), as new species A, tentatively hypothesized that *M. sylvicola* was a relatively primitive species of *Mimagoniates* with respect to caudal-fin pump evolution. They placed *M. sylvicola* in an unresolved polytomy in their phylogenetic diagram along with *M. barberi* and *M. inequalis* and a monophyletic line leading to *M. lateralis, M. microlepis* and their new species B and C. This hypothesis was based on the information that apparently fully adult males of all three species, *M. barberi, M. inequalis* and their new species A (here = *M. sylvicola*), lack the more derived chambered, caudal-fin ray pump of the other four species. Compare caudal pump structures in Figs. 2 and 3 with those in Figs. 4 and 5.

Evidence taken from a specimen of *M. sylvicola,* USNM 300633, SL 32.5 mm, subsequently available to us from near Porto Seguro, Bahia, showed that the caudal gland matures with a well-developed pump chamber, (compare Figs. 11 and 12). However, this species lacks the caudal-fin hooks found in the more derived species, *M. rheocharis,* described below, and in *M. microlepis* (compare Figs. 5, 11, 12, and 24). This information would place *M. sylvicola* in a trichotomy, Fig. 1, with *M. lateralis* and a monophyletic line leading to the two species with caudal-fin hooks. This hypothesis would leave *M. inequalis, M. barberi* and a monophyletic line leading to the species of *Mimagoniates* with more derived caudal pumps in a trichotomy at a lower level in the phylogenetic diagram (Fig. 1). If this relationship can be supported by further phylogenetic evidence, then the biogeo-

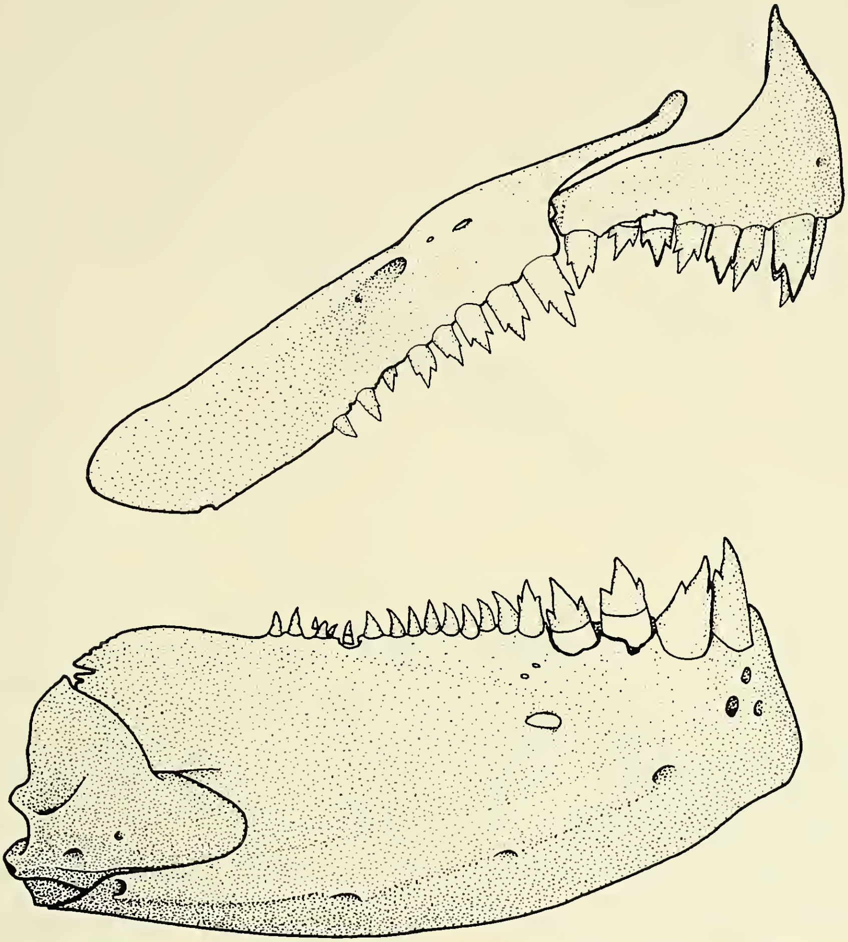

Fig. 13. *Mimagoniates sylvicola,* new species, paratype, jaws and dentition of an adult male, lateral view, right side, anterior at right. SL 29.3 mm, USNM 276557, same locality data as holotype, Fig. 7. For explanation see text under Description of *M. sylvicola.*

graphic comments of Weitzman et al. (1988: 412, 413) need some alteration (see section on biogeography below).

It was noted in the diagnosis above that adult males and females of *M. sylvicola* from Cumuruxatiba (MZUSP 28815, 28816, 28817, 36612 and USNM 276547, 276556, 276557), differ in body depth from adult males and females of *M. lateralis* from the Santos region (CAS 36634, MZUSP 40276, 40277, USNM 226468, 254268, 257200, and 257202). Forty five males of *M. sylvicola* and 22 males of *M. lateralis* were significantly different ($F_{0.05,(1,63)} = 49.75$, $P < 0.000$) in an analysis of covariance for body depth on SL in an F-ratio test for homogeneity of slopes, Fig. 15. Body depth ratios of SL useful for identification of fully or near fully mature males (at or above 23.0 mm SL) are as follows: $n = 12$ specimens of *M. sylvicola* from Cumuruxatiba and near Porto Seguro, $\bar{x} = 3.6$, range = 3.4–3.8 and $n = 23$ specimens of *M. lateralis* from near Santos and Município de Cananéia, $\bar{x} = 4.3$,

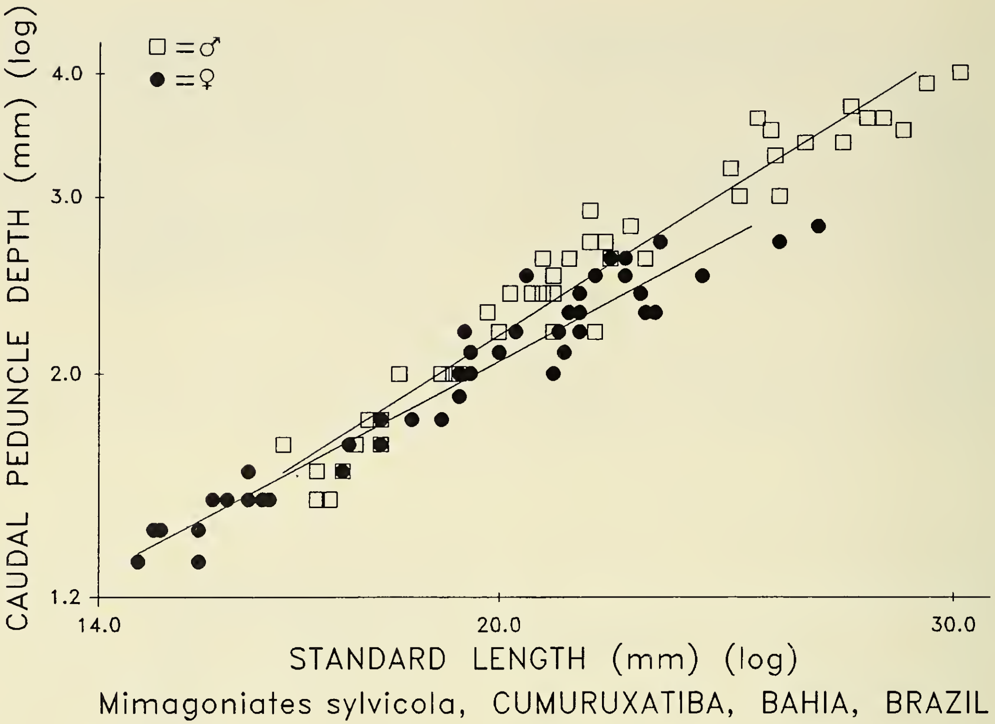

Fig. 14. *Mimagoniates sylvicola,* new species, caudal peduncle depth as a function of SL by sex. Plot axes are logarithmic. Logarithmic regression equation for 45 males: ($Y = -4.089 + 1.625X$), for 45 females: ($Y = -3.377 + 1.368X$). Immature males and juveniles may be included in the category designated female. For explanation see under Sexual dimorphism in text of *M. sylvicola.*

range = 3.8–5.1. The shorter males in these size ranges accounted for most of the overlap.

In a similar covariance analysis for slopes, 45 adult females of *M. sylvicola* and 26 females of *M. lateralis* from the same population samples as the males discussed above, also displayed significant difference in body depth ($F_{0.05,\,(1,\,67)} = 16.3$, $P < 0.001$) (Fig. 16).

The number of branched anal-fin rays in the two species was significantly different ($t = 22.012$, $P < 0.00$ in a two-sample, two-tailed t-test), although there was some overlap in counts: $n = 90$ specimens of *M. sylvicola* from near Cumuruxatiba (same lots as listed above), range = 23–26, $\bar{x} = 24.8$, SD = 0.7728 and $n = 91$ specimens of *M. lateralis* from near Santos and Município Cananéia (same lots as listed above), $\bar{x} = 27.9$, range = 25–31, SD = 1.0899.

Ecology.—Little is known about the ecology of this species. Most of the streams in which it was captured were relatively slow moving, with little gradient. They were approximately 4 to 6 meters wide, to 1.5 meters deep and surrounded by vegetation, usually trees of a few to many meters high. The water varied from clear to black (tea color). The fish occurred in depths of 0.1 to about 0.5 meters usually in areas of little current over white sandy, rocky or dark mud bottoms. They occurred in both sunlight or shaded areas, most often near shore, especially near emergent or submerged vegetation where almost immediate cover could

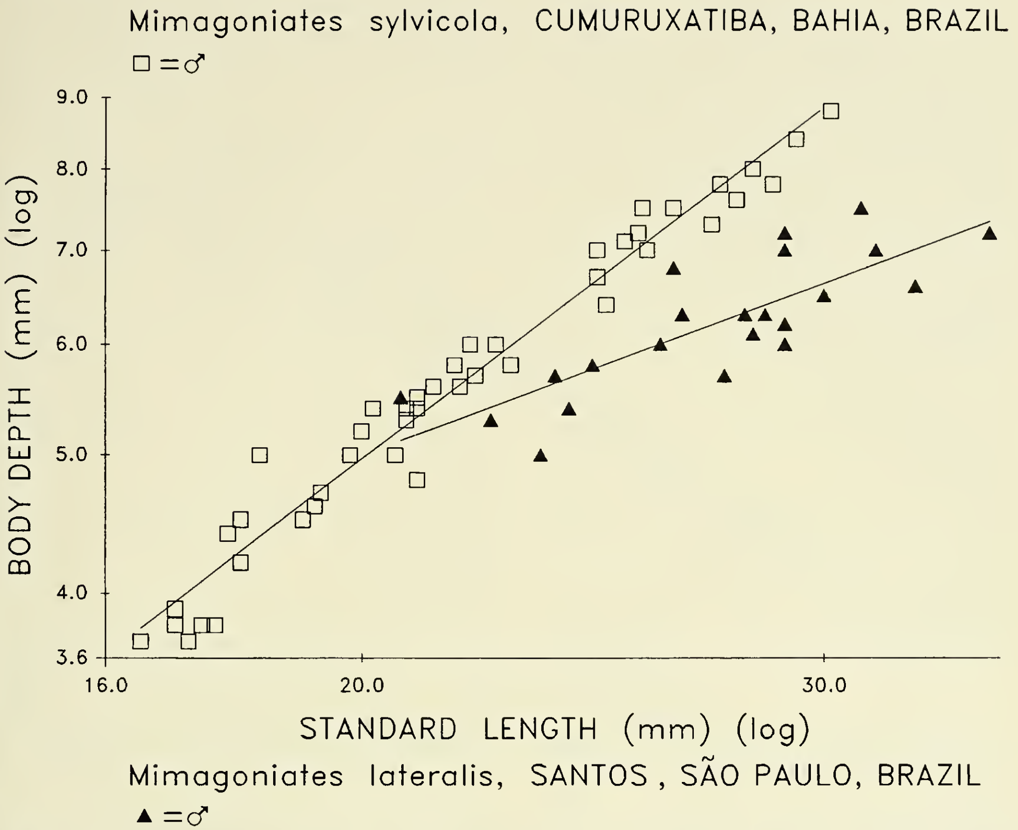

Fig. 15. *Mimagoniates sylvicola* and *Mimagoniates lateralis,* body depth as a function of standard length for young to adult males. Plot axes are logarithmic. Logarithmic regression equation for 45 males of *M. sylvicola*: (Y = −2.650 + 1.420X) and 22 males of *M. lateralis*: (Y = 0.473 + 0.695X). For explanation see Discussion under *M. sylvicola.*

be taken from predators such as large cichlids or the characid *Oligosarcus.*

Specimens of *M. sylvicola,* now MZUSP 28817 and USNM 276557, were collected 22 March 1985 in a well-shaded forest rivulet less than 1 meter wide and about 20–30 cm deep in most places. This creek was in a ravine of a mostly uncut, undisturbed tall forest, 1 or 2 km from the Atlantic coast, about 17 km from Cumuruxatiba, Bahia. The stream bottom consisted of forest litter, rocks, soil and sand with a mild nearly 0° to 30° gradient, well covered by riparian vegetation in many places. The water was tea colored. Other fish species taken at this site were *Rachoviscus graciliceps,* species of *Astyanax, Characidium, Aspidoras, Heptapterus,* a gobiid and a hypoptopomine loricariid catfish.

Mimagoniates rheocharis, new species
Figs. 17–28, Table 2

Species B.—Weitzman et al., 1988:figs. 6, 10, 23 [phylogeny and biogeography].

Holotype.—MZUSP 40278, male, SL 47.3 mm, Brazil, Santa Catarina, Município de Praia Grande, rio Faxinalzinho at Mãe dos Homens, near Praia Grande, approximately

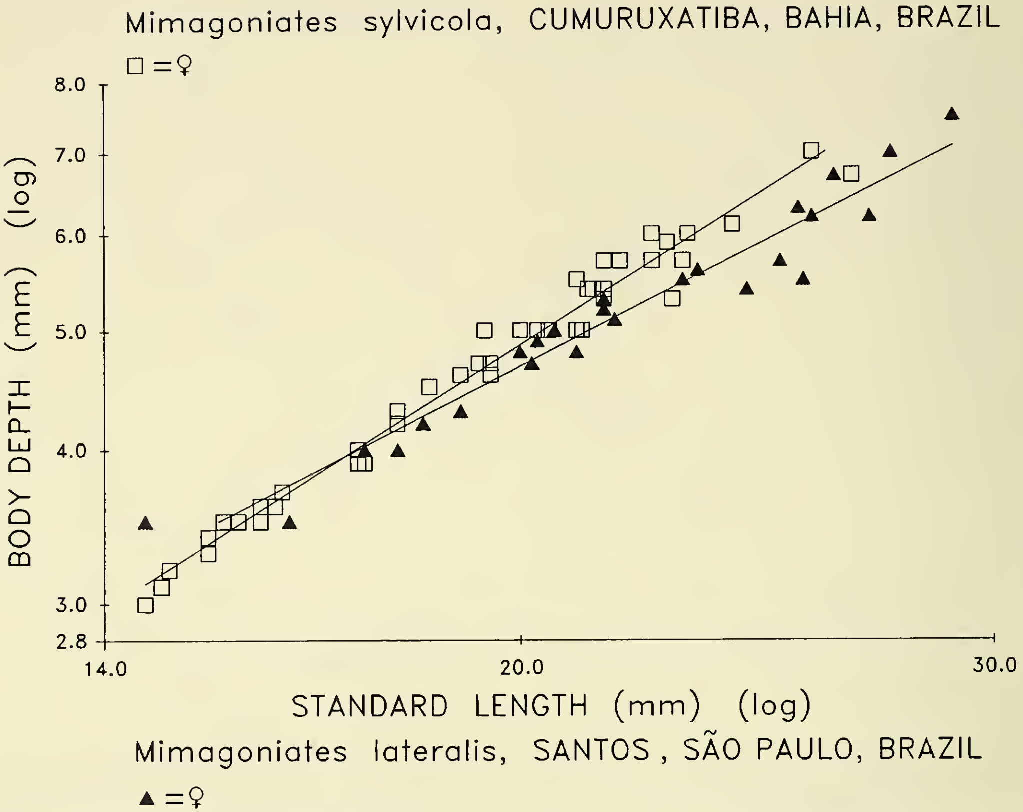

Fig. 16. *Mimagoniates sylvicola* and *Mimagoniates lateralis,* body depth as a function of standard length for young to adult females. Plot axes are logarithmic. Logarithmic regression equation for 45 females of *M. sylvicola*: (Y = −2.567 + 1.385X) and 26 females of *M. lateralis*: (Y = −1.807 + 1.118X). For explanation see Discussion under *M. sylvicola.*

29°20′S, 14°40′W, 9 Jun 1985; C. A. S. de Lucena, R. E. Reis, and L. R. Malabarba.

Paratypes.—Following 2 lots of immatures to adults collected with holotype: MCP 13616, spms. 3, SL 24.3–40.8 mm; USNM 279878, spms. 3, SL 33.3–47.8 mm. Following 3 lots of immature to adult paratypes all collected 7 Jun 1985 by C. A. S. de Lucena and party: Brazil, Santa Catarina, Município de Nova Veneza, rio Jordão at Jordão Alto, approximately 28°36′S, 49°28′W, MCP 13617, spms. 83, SL 21.9–39.0 mm; MZUSP 40279, spms. 81, SL 22.4–42.8 mm; USNM 270879, spms. 89, SL 22.8–49.0 mm. Following 3 lots of immature to adults all collected by R. M. C. Castro 13 Feb 1988: Brazil, Santa Catarina, Município de Praia Grande, tributary of rio Grande approximately 29°20′S, 49°40′W, MZUSP 40280, spms. 29, SL 13.5–38.4 mm; USNM 306339, spms. 18, SL 17.0–40.0; spms. 2 to R. M. C. Castro, SL 28.0–31.30 mm. MZUSP 40281, SL 41.8 mm (mature male), Brazil, Rio Grande do Sul, Município de Osório, arroio das Pedras, approximately 29°52′S, 50°19′W, 11 Feb 1988, R. M. C. Castro. MCP 13613 spms. 7, SL 27.5–31.3 mm, Brazil, Município de Osório, arroio Água Parada, tributary to rio Maquiné, in Maquiné, approximately 29°40′S, 50°11′W, 10 Oct 1989, R. E. Reis, S. O. Kullander, L. R. Malabarba and J. Pozzi. MCP 10806, SL 39.5 mm (mature male), Brazil, Rio Grande do Sul, Município de

Torres, tributary of rio Três Furquilhas, Chapéu, approximately 29°19′S, 49°44′W, 25 May 1986, C. A. S. Lucena, R. E. Reis, and L. R. Malabarba.

Diagnosis.—Mimagoniates rheocharis may be separated from all other species of *Mimagoniates* by use of the key provided above and the characters described and discussed below. *Mimagoniates rheocharis* is sympatric with and apparently at least partly syntopic with *M. microlepis* in south coastal Santa Catarina. It is also sympatric and syntopic with *M. microlepis* in the rio Maquiné drainage. The southern distribution of *M. rheocharis* (rio Maquiné drainage and streams immediately surrounding Osório in Rio Grande do Sul) is adjacent to the northeastern limit (rio Gravataí drainage) of *M. inequalis* where these two species abut and appear to be allopatric (see the Biogeography section and phylogenetic discussion in the Discussion section below). The possible relationships of *M. rheocharis* to *M. inequalis* or *M. microlepis* is uncertain and perhaps complex but the following series of characters distinguish *M. rheocharis* from one or the other of these species or, in some cases, both of them. Because the comparisons are somewhat complex, for clarity the two compared species are treated separately.

Mimagoniates rheocharis may be distinguished from *M. microlepis,* by the following characters (see also the statistical analyses of overlapping characters under Statistical Comparisons below). Scale rows around caudal peduncle 19–23 (15–18 for *M. microlepis*); scale rows between dorsal-fin and anal-fin origins 17–22, rarely 17 (14–17, rarely 17 for *M. microlepis*); total lateral series scale count shows broad overlap between both species, 41–48 (42–49 for *M. microlepis*) but in at least one population comparison of *M. rheocharis* and *M. microlepis* showed a statistically significant difference (see the statistical comparisons below); branched dorsal-fin ray count 8–12, usually 9–10, rarely 8 (7–9, rarely 9 for *M. microlepis*); branched anal-fin ray count 23–29, usually 24–26 and rarely 28 or 29 (26–33, usually 28–31 and rarely 26 or 27 for *M. microlepis*); total vertebral count 35–40, usually 36–38, rarely 39 or 40 (38–41, usually 39–40, rarely 38 in *M. microlepis*); tenth and eleventh principal caudal-fin rays of adult males with small, little developed hooks posterior to caudal organ but with sturdy hooks on ray 11 along ventral border of expanded ray segments of caudal organ, Fig. 24 (adult male *M. microlepis* with well-developed hooks on caudal-fin rays 7–12 and no sturdy hooks on principal ray 11 along ventral border of expanded ray segments of caudal organ, note, some populations with few or no hooks on rays 7 and/or 12); preserved and live colors in part different between both species, but variation in live colors among various population samples of *M. microlepis* make comparisons difficult.

A few life color characters appear consistently different in fully mature males: pelvic-fin rays and membranes of adult males distally white (adult male *M. microlepis* with yellow and/or black pigment of pelvic fins continuous to edge of fin where fin bordered by narrow band of white); anal fin posterior to anterior lobe bordered by broad band of deep yellow pigment, very little to no black pigment on fin (adult male *M. microlepis* with posterior portion of anal fin ventrally bordered by narrow band of black pigment, none or very little yellow pigment).

As treated below in the Discussion, there are some, perhaps plesiomorphic, body shape similarities shared between *M. rheocharis* and *M. inequalis.* Furthermore, *M. rheocharis* appears to have the caudal peduncle and body depths for both sexes intermediate between those of *M. microlepis* and *M. inequalis*; see Figs. 17 and 27. Certain aspects of the caudal pump morphology of *M. rheocharis* could also be interpreted as intermediate. This suggests the possibility that *M. rheocharis* might be closely related to *M. inequalis* rather than to *M. mi-*

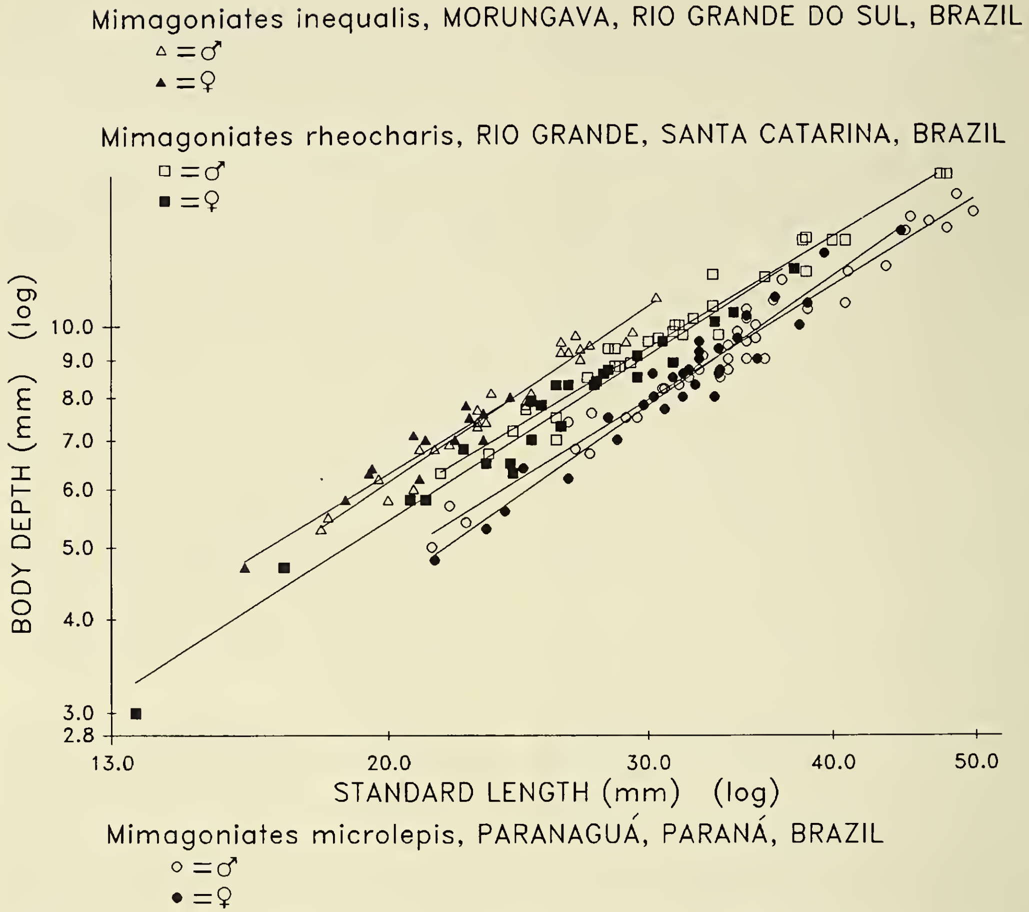

Fig. 17. *Mimagoniates rheocharis, M. microlepis* and *M. inequalis,* body depth as a function of SL by species and sex. Plot axes are logarithmic. Logarithmic regression equation for 31 males of *M. rheocharis*: (Y = −1.846 + 1.199X), 25 females or this species: (Y = −2.115 + 1.271X); for 39 males of *M. microlepis*: (Y = −2.130 + 1.235X) and for 31 females of the later species: (Y = −2.705 + 1.399X); and for 26 males of *M. inequalis*: (Y = −2.230 + 1.3499X), 14 females of this species: (Y = −1.812 + 1.2187X). For explanation see Diagnosis, Sexual dimorphism, Discussion and Description under *M. rheocharis.*

crolepis or even derived by introgression from ancestral sympatric populations of *M. microlepis* and *M. inequalis* in a manner suggested by Hubbs (1955:19) for freshwater fishes in North America. However, not all counts or body proportions of *M. rheocharis* are intermediate between the two species and we question the intermediacy of *M. rheocharis* based on tentative polarity and parsimony analyses of the available data (see Discussion below). In any case, the similarities of many features, especially of immature or just maturing specimens, shared between *M. rheocharis* and *M. inequalis* makes it a practical necessity to describe the differences in some detail between the population samples at hand of these two species. The phylogenetic polarities of most of these characters are relatively uncertain for those species possessing them. Therefore their use as synapomorphies suggesting relationships to and/or among species of *Mimagoniates* that may share them remains to be more fully investigated. Tentatively, many of these

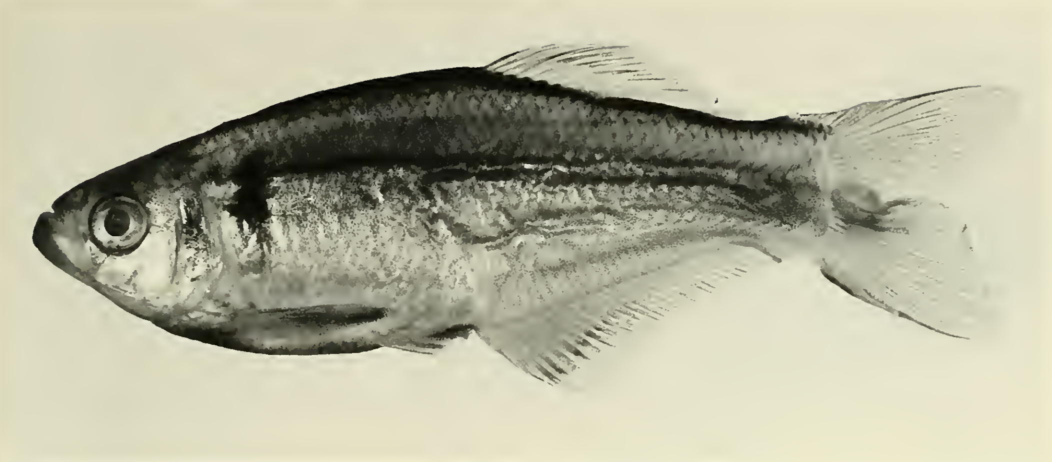

Fig. 18. *Mimagoniates rheocharis,* new species, holotype, MZUSP 40278, male, SL 47.3 mm; Brazil, Santa Catarina, rio Faxinalzinho at Mãe dos Homens, near Praia Grande.

characters appear plesiomorphic for *M. inequalis* when the latter is compared to *M. rheocharis* or *M. microlepis.*

For convenience the following same characters as those treated above to separate *M. rheocharis* and *M. microlepis* are considered for comparison between *M. rheocharis* and *M. inequalis* even though not all these characters are diagnostic for separation of the latter two species (see also the section below on Statistical Comparisons). Scale rows around caudal peduncle = 19–23 for *M. rheocharis* (16–19 for *M. inequalis*) (both species commonly with a count of 19); scale

Fig. 19. *Mimagoniates rheocharis,* new species, paratype, USNM 306339, female, SL 34.3 mm; Brazil, tributary to rio Grande, Santa Catarina.

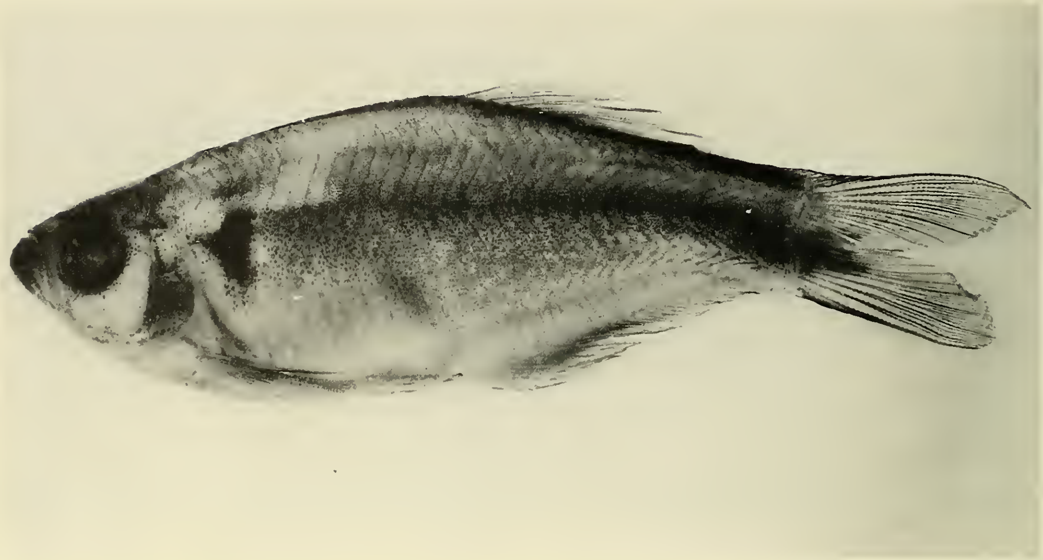

Fig. 20. *Mimagoniates rheocharis,* new species, paratype, MZUSP 40281, male, SL 41.8 mm; Brazil, Rio Grande do Sul, arroio das Pedras, near Osório.

rows between dorsal-fin and anal-fin origins = 17–22 (16–18 for *M. inequalis*); lateral series scale count = 41–48, rarely 41 (36–41 for *M. inequalis,* 41 being uncommon); branched dorsal-fin ray count 8–12, usually 9 or 10, only occasionally 8 (8–9, rarely 9 for *M. inequalis*); branched anal-fin ray count 23–29, usually 24–26, rarely 28 or 29 (24–30, rarely 24 for *M. inequalis*), these counts significantly different statistically between some population samples but not in others (see statistical analyses below); total vertebral count 35–40, rarely 39–40 (36–39 for *M. inequalis*); principal caudal-fin rays 10 and 11 of adult males with small, little developed hooks posterior to caudal-fin organ, see Fig. 24 (adult male of *M. inequalis* without hooks on caudal-fin rays 10 and 11); preserved color patterns essentially indistinguishable between the two species and we have not been able to study the live color patterns of adult males where differences between the species would most likely be present.

Description.—Table 2 presents morphometrics of the holotype and paratypes. Except where noted, the entire description refers to the population sample from near Praia Grande, southern Santa Catarina. These collections were treated statistically as one population sample in an attempt to represent the species as a whole from this area. Counts and ratios of measurements for other population samples taken from a tributary of the rio Grande are given only when they differ from those from near Praia Grande.

Body compressed, relatively deep, especially near dorsal-fin origin; body deepest at vertical line through anal-fin origin. Predorsal body profile relatively arched in adult males, less so in adult females and immatures which have predorsal profile gently convex to tip of snout. Body profile elevated at dorsal-fin origin, still strongly arched in males, less so in females and juveniles. Dorsal body profile nearly straight along dorsal-fin base to adipose fin. Body profile posterior to adipose fin somewhat concave dorsal to caudal peduncle, ending at origin of procurrent caudal-fin rays. Dorsal-fin origin nearer to caudal-fin base than to snout tip.

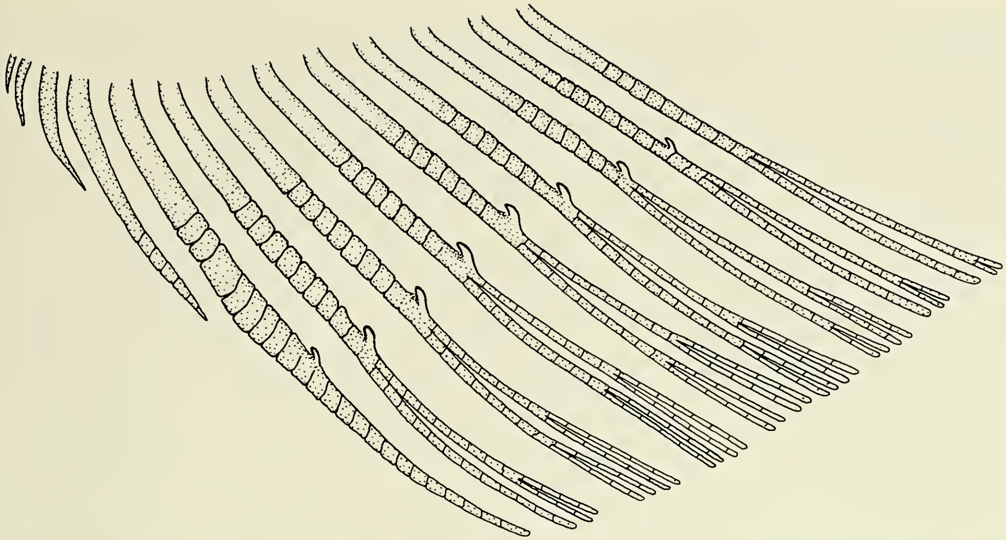

Fig. 21. *Mimagoniates rheocharis,* new species, paratype, anterior 13 anal-fin rays of an adult male, lateral view, anterior is at left. USNM 279879, SL 45.4 mm; Brazil, Santa Catarina, rio Jordão at Jordão Alto. For explanation see Description under *M. rheocharis.*

Ventral body profile strongly convex in adult males from anterior tip of lower jaw to origin of pelvic fins, less strongly convex in females and juveniles. Belly profile in adult males slightly concave to anal-fin origin, straight or nearly so in females and juveniles. Body profile along anal-fin base in males slightly concave at anterior base in region of anterior lobe of anal fin; straight along base of remainder of fin in males and along entire anal-fin base in females and juveniles. Ventral profile of caudal peduncle convex in adult males when anterior 5 or 6 strongly developed procurrent ventral caudal-fin rays are included in that profile; slightly concave or nearly straight in females and juveniles.

Head and snout of moderate size in proportion to body length. Lower jaw protruding, slightly anterior to upper jaw. Lower jaw of adult males thick and heavy compared to that of females and juveniles. Mouth angled posteroventrally from anterior tip of snout to posterior part of mandibular joint. Maxilla long, extending to a point ventral to a horizontal line drawn from ventral border of eye in juveniles and adults of both sexes. Maxilla extends posteriorly to a point anterior to vertical line drawn through anterior border of pupil of eye.

Dorsal-fin rays ii,9 (unbranched rays ii in all specimens, branched rays $\bar{x} = 8.9$, range = 8–10, $n = 56$); posterior ray not split to its base and counted as 1. Adipose fin present, slender. Anal-fin rays iv,26 (iv or v, usually iv, $\bar{x} = 26.8$ for branched rays, range = 25–29, $n = 56$); posterior ray split to its base and counted as 1. Anal fin with moderately developed lobe anteriorly (Figs. 18, 19). Lobe includes fourth or fifth undivided ray and first 3 divided rays. Anal fin of sexually mature males with bilateral hooks, 1 on each side, on anterior unbranched ray iv or v, whichever occurs just before branched rays (Fig. 21). Usually anterior 7 branched fin rays with bilateral hooks, 1 set for each ray. Pectoral-fin rays i,10 (unbranched ray i in all specimens, branched rays $\bar{x} = 10.1$, range 10–11, $n = 56$). Posterior tips of longest pectoral-fin rays extend posteriorly beyond origin of pelvic fins; fins of about equal extent in both sexes. Pectoral-fin rays with-

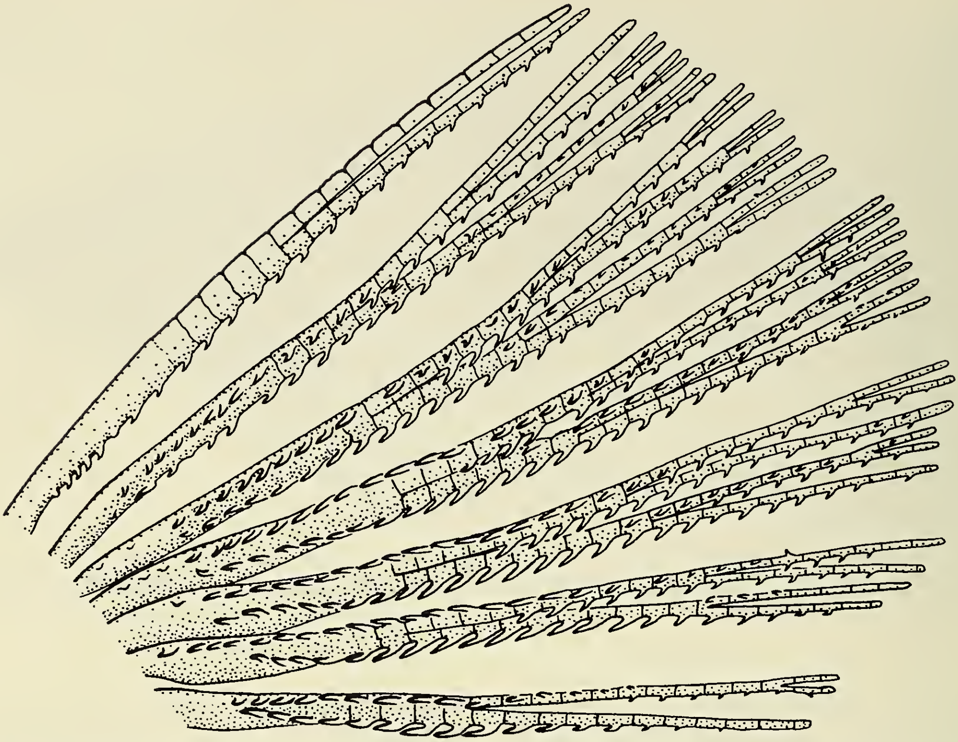

Fig. 22. *Mimagoniates rheocharis,* new species, paratype, pelvic fin of adult male, ventral view, left side, anterior at left, medial fin ray at bottom. USNM 279879, SL 45.4 mm; same locality data as specimen in Fig. 21.

out hooks. Pelvic fin rays 8 in all specimens. Pelvic fin with anterior (first) ray branched once, branches remaining close together and entire ray tapering as in most characiforms that have anterior ray unbranched (Fig. 22). Sexually mature, large adult males with over 400 hooks on each pelvic fin.

Principal caudal-fin ray count 10/9 in all specimens, ($n = 56$). Fin rays modified in association with caudal pheromone pump as in Figs. 23 and 24. Fin rays modified more like those in *M. microlepis* than any other species of *Mimagoniates* (Fig. 5). Caudal-fin rays 10 and 11 with small bony hooks. Ventral borders of 4 anterior expanded ray segments of ray 11, which form anterior external wall of dorsal portion of pump chamber, with about 4 short but large hooks, 2 middle hooks often bicornate, others 1 hooked.

Scales cycloid, with few radii along posterior border. Terminal scale of modified caudal-fin series without exaggerated radii (Fig. 24b).

Lateral line incomplete, perforated scales 7 ($\bar{x} = 6.7$, range 5–9, $n = 48$). Lateral series scales 45 ($\bar{x} = 44.3$, range = 41–48, $n = 48$). Predorsal scales = 22 ($\bar{x} = 22.3$, range = 21–24, $n = 46$). Scale rows between dorsal-fin and anal-fin origins 19 ($\bar{x} = 18.8$, range = 17–21, $n = 55$). Scale rows around caudal peduncle 20 ($\bar{x} = 19.7$, range = 19–22, $n = 46$).

Premaxillary teeth in 2 distinct rows, Fig. 25. Larger and smaller teeth tricuspid in all large specimens, sometimes in smaller specimens small teeth bicuspid or conical. Outer row teeth 5 ($\bar{x} = 6.2$, range 5–8, $n = 55$). Inner row teeth few, 3 ($\bar{x} = 2.1$, range = 1–3, $n = 55$). Outer and inner row premaxil-

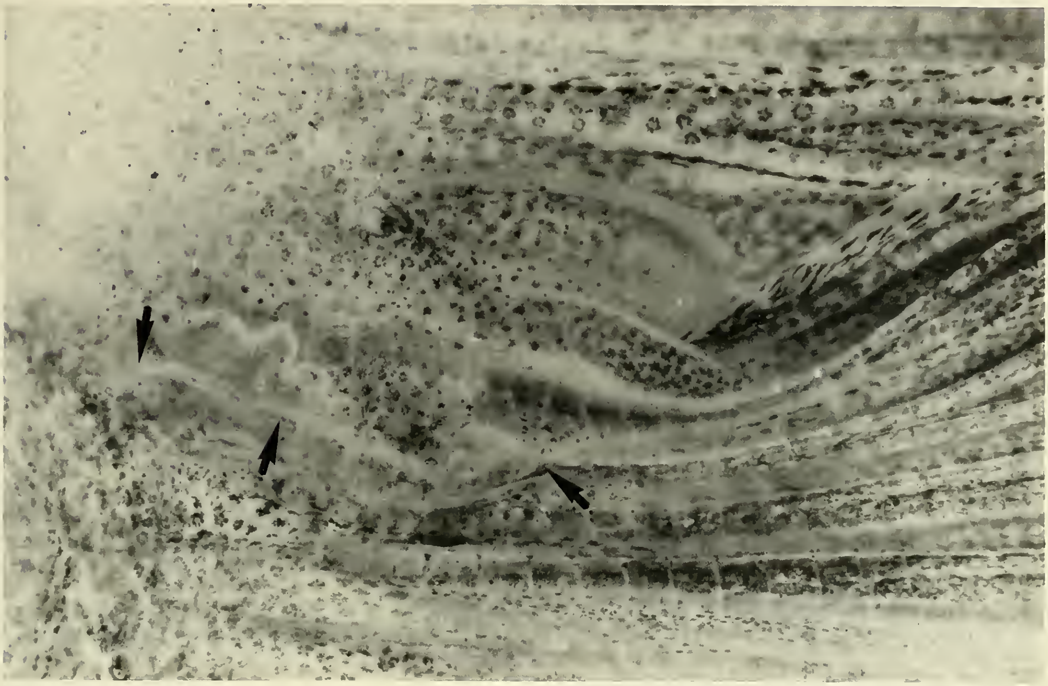

Fig. 23. *Mimagoniates rheocharis,* new species, paratype, unstained central basal region of caudal fin and adjacent caudal peduncle of adult male, lateral view, left side, anterior at left. USNM 279879, SL 49.0 mm; same locality data as specimen in Fig. 21. Arrow at left indicates anterior intake region of pump chamber. Middle arrow indicates region of lateral slit with ray half of principal ray 11 just dorsal to arrow tip. Arrow at right points to opening of posterior exhaust vent of pump chamber. Note that in this species pump chamber not formed into an obvious cylindrical tube as that of *M. microlepis,* Fig. 3. Glandular tissue surrounding chamber openings in this photograph obscure details of pump.

lary teeth somewhat compressed compared to most "tetragonopterine" characid teeth which are often circular in cross section. Maxillary teeth 8 ($\bar{x}$ = 5.4, range = 3–8, larger specimens usually with higher counts, n = 55). All maxillary teeth usually tricuspid in large sepcimens; small specimens with posterior maxillary teeth often conical. Dentary with 4 large tricuspid teeth in all specimens, smaller posterior teeth 12 ($\bar{x}$ = 8.4, range = 5–12, almost always greater number of teeth in largest specimens, anterior small maxillary teeth tricuspid, posterior ones conic, n = 54). Maxillary and dentary teeth shaped much like premaxillary teeth described above. No significant difference in tooth number found between males and females.

Vertebrae 38 ($\bar{x}$ = 38, range = 37–40, n = 107). Dorsal limb gill rakers 7 ($\bar{x}$ = 6.6, range = 6–8, n = 54); ventral limb gill rakers 12 ($\bar{x}$ = 11.7, range = 11–13, n = 54). Branchiostegal rays 4, in 3 cleared and stained specimens, 3 rays originating on anterior ceratohyal and 1 ray from posterior ceratohyal.

Color in alcohol.—See Figs. 18–20 for preserved color pattern of males and females. Body pale to medium brown, pale yellowish brown ventrally, much darker dorsally. Lateral body stripe diffuse in both sexes, especially anteriorly. Stripe extending from vertical humeral spot posteriorly to caudal fin and onto dorsal region of ventral caudal-fin lobe and small part of dorsal caudal-fin lobe. Lateral stripe extends over all

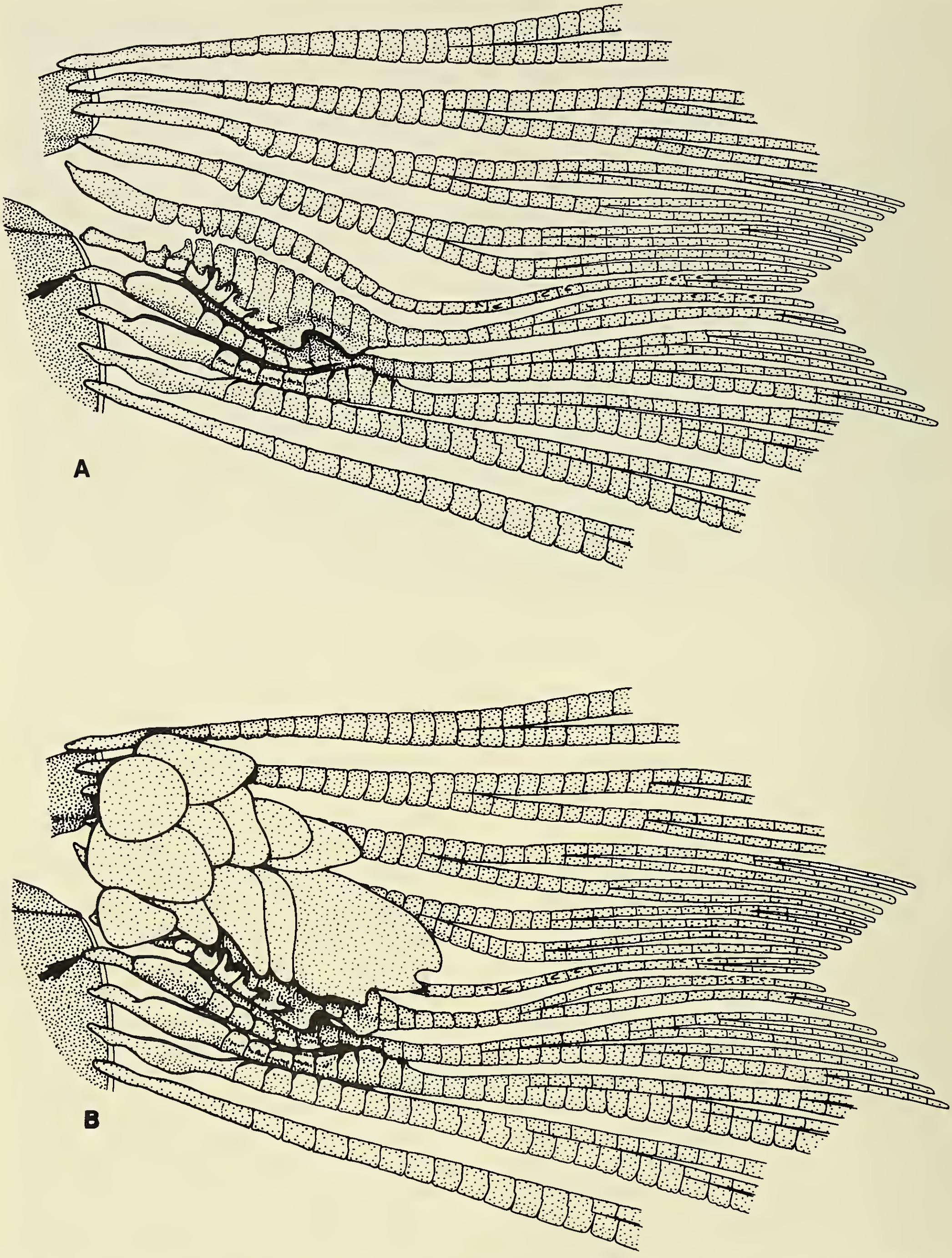

Fig. 24. *Mimagoniates rheocharis,* new species, paratype, osteology of central basal region of caudal skeleton, principal fin rays 6–15, of an adult male, lateral views, left side, anterior at left. USNM 279879, SL 45.4 mm, same locality data as specimen in Fig. 21. Principal ray 12 indicated by arrow. (A) Illustrates caudal pump region. (B) illustrates relationship of modified dorsal caudal-fin lobe squamation to caudal pump.

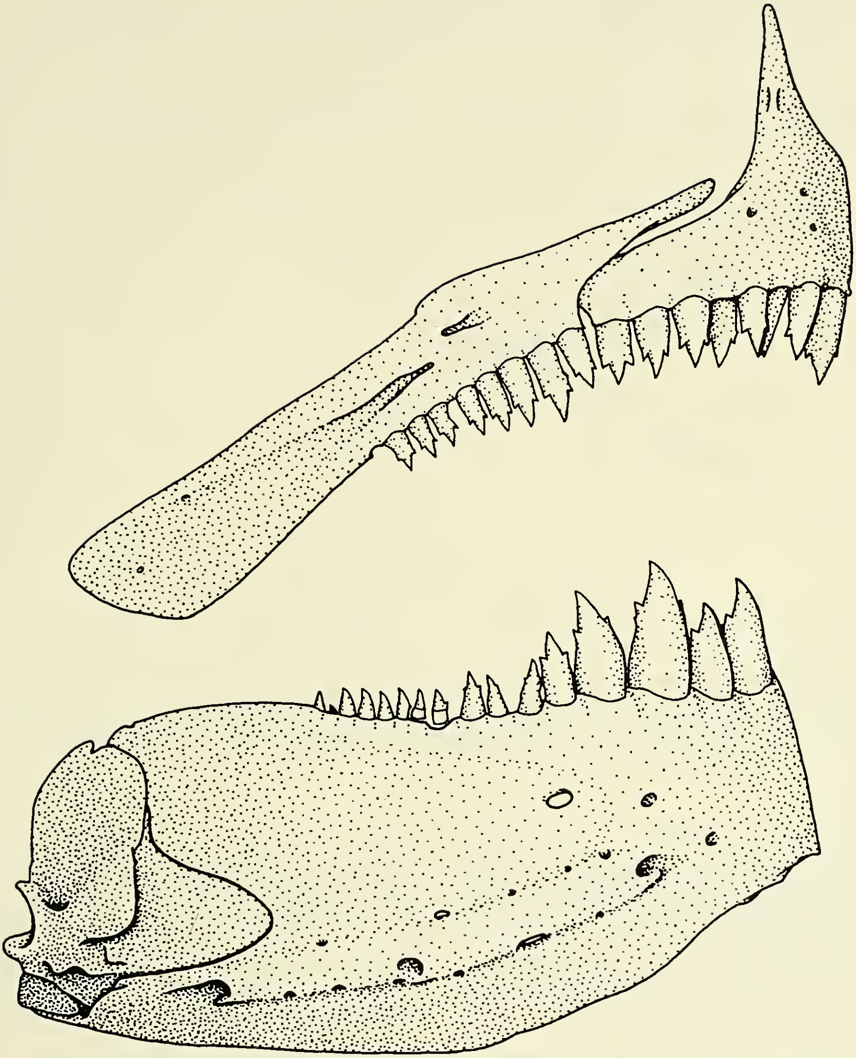

Fig. 25. *Mimagoniates rheocharis*, new species, paratype, jaws and dentition of adult male, lateral view, right side, anterior at right. USNM 279879, SL 45.4 mm, same locality data as in Fig. 21. For explanation see text Description under *M. rheocharis.*

caudal gland structures, including those derived from dorsal caudal-fin lobe such as modified caudal squamation. Stripe especially dark on principal rays 10, 11 and 12, less so on ray 13. Humeral spot vertically elongate, especially in sexually mature males. Remainder of caudal fin dusky because of scattered dark chromatophores. Dorsal border of first principal caudal-fin ray and ventral border of nineteenth principal caudal-fin ray black. Utmost dorsal body surface black, forming a narrow stripe extending from supraoccipital region to base of dorsal procurrent rays of caudal fin. Remainder of dorsal body surface ventral to lateral body stripe pale brown.

Pectoral, pelvic, dorsal and anal fins dusky with scattered dark chromatophores along fin rays and membranes. Anal fin with a dark elongate stripe running length of fin.

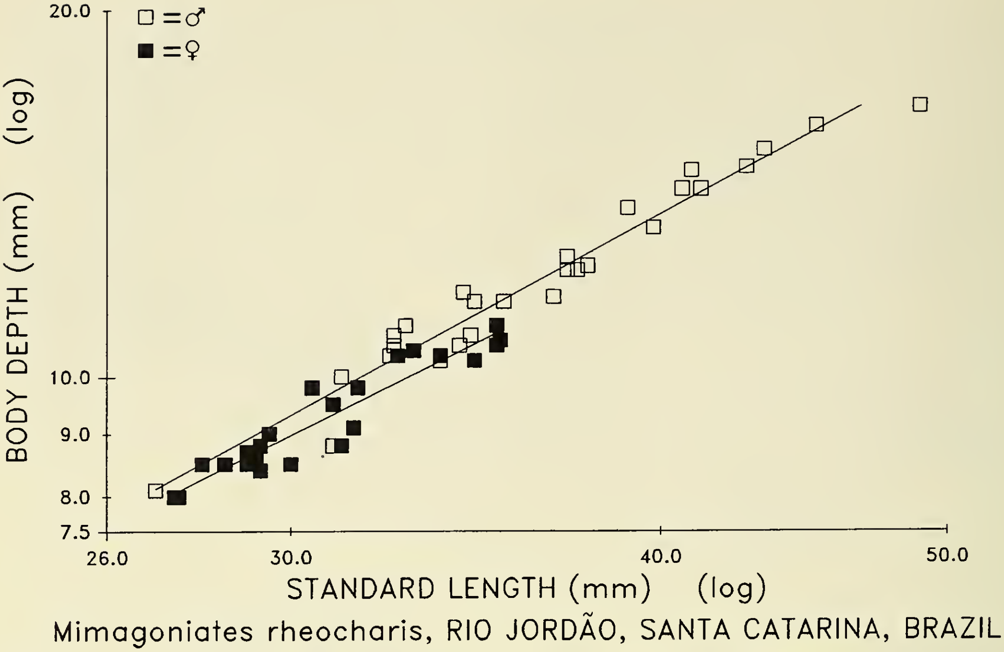

Fig. 26. *Mimagoniates rheocharis,* new species, paratypes, body depth as a function of SL by sex. Plot axes are logarithmic. Logarithmic regression equation for 27 males of *M. rheocharis*: (Y = −2.190 + 1.300X) and for 23 females of this species: (Y = −1.831 + 1.183X). For explanation see Sexual dimorphism under *M. rheocharis.*

Stripe width about one-fourth height of anal fin anteriorly and about one-half fin's height posteriorly. Stripe of nearly uniform width throughout its length, but fin height changes, being considerably shorter posteriorly. In sexually mature males stripe considerably darker anteriorly, especially dorsal to anterior anal-fin lobe which appears relatively hyaline. Dorsal-fin with a horizontal dark stripe in adult males and females extending posteriorly from about mid-length of anterior elongate undivided ray to posterior tips of terminal two dorsal-fin rays. Stripe usually narrow, less than one-eighth height of dorsal fin at latter's longest measurement. Width and density of stripe variable depending on sex and sexual maturity. Preserved males sometimes with posterior portion of stripe diffuse. Adipose fin dusky with scattered dark chromatophores.

Head dark brown around mouth and on dorsal surface of snout, between eyes, dorsum of cranium and nape. Mental area of lower jaw dark brown. Head area posterior to circumorbitals and extending ventrally from parietal region, across dorsal opercular region dark brown. Dark area continues ventrally across posterior region of opercular bone to just reach interopercular bone; looks like an anteriorly misplaced humeral spot. Iris dorsal to pupil dark brown, most of remainder of iris silvery. Circumorbitals silvery if guanine preserved, pale yellowish brown if guanine destroyed by formalin. Dark brown chromatophores scattered evenly through circumorbital area. Anterior area of opercle, all of preopercle, and branchiostegal rays silvery or pale brown, without much dark brown pigment.

Color in life.—Life colors described here taken from a 35 mm color slide made by Ricardo M. C. Castro of an adult male 41.8 mm SL (MZUSP 40281). See also black and white photograph of this specimen in pre-

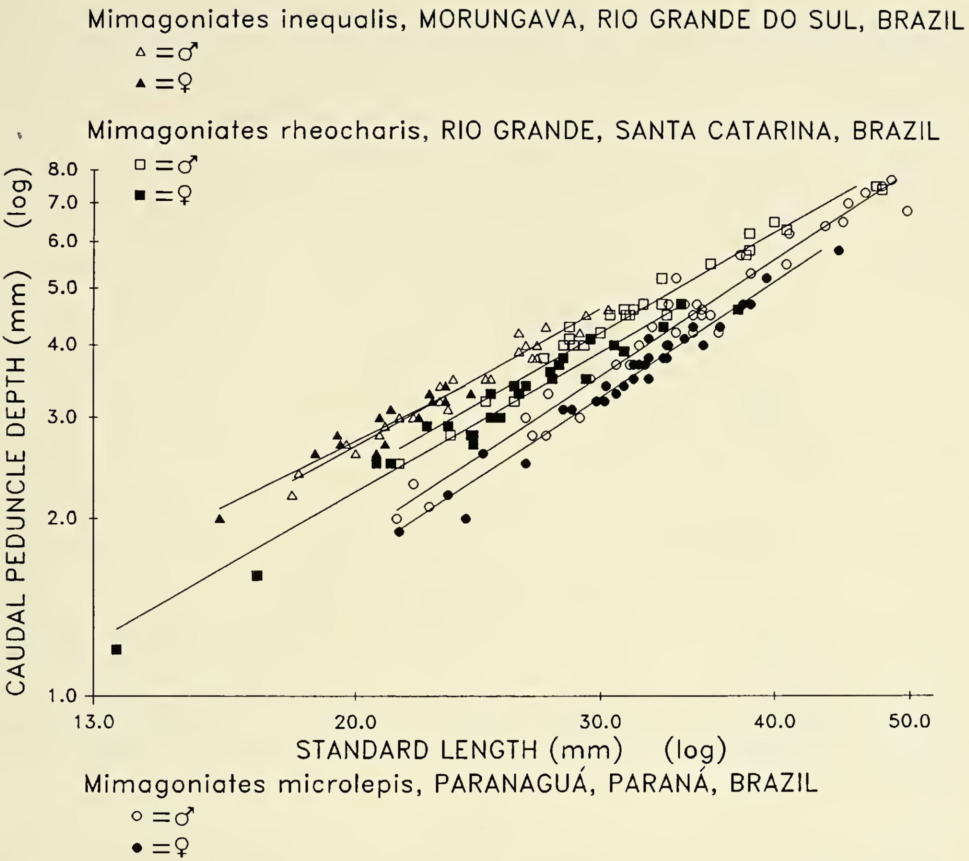

Fig. 27. *Mimagoniates rheocharis, M. microlepis* and *M. inequalis* caudal peduncle depth as a function of SL by species and sex. Plot axes are logarithmic. Logarithmic regression equation for 31 males of *M. rheocharis*: ($Y = -4.222 + 1.588X$), for 26 females of the same species: ($Y = -3.311 + 1.374X$); for 40 males of *M. microlepis*: ($Y = -4.151 + 1.592X$) and for 30 females of the later species: ($Y = -3.239 + 1.374X$); and for 26 males of *M. inequalis*: ($Y = -3.021 + 1.3375X$), 14 females of this species; ($Y = -2.625 + 1.2116X$). For explanation see Diagnosis, Sexual dimorphism, Discussion and Description under *M. rheocharis.*

servative, Fig. 20. Specimen photographed just after capture from a clear water stream surrounded by vegetation. Site located immediately north of city of Osório, Rio Grande do Sul. Sides of body pale silvery blue. Broad lateral body stripe somewhat deeper silvery blue from humeral spot to caudal peduncle termination. Just dorsal to silvery blue color of body sides, back with a narrow dark brown line extending from parietal region of head to just ventral to adipose fin. Lateral portion of back between narrow brown line and dorsomedian narrow dark brown line extending across dorsalmost portion of back, a brownish yellow green color. Dorsal region of caudal peduncle nearly yellow. Ventral abdominal area, most of lower jaw, ventral opercular area, branchiostegal rays and their membranes silvery white. Dark pigment of head similar to that described for preserved specimens except that dorsal region of opercle appears silvery blue. Dorsal caudal-fin lobe and principal caudal-fin rays 14–16 on ventral caudal-fin lobe bright yellow, except for black proximal half of ray 14. This black pigment continuous with black pigment surrounding structures of caudal phero-

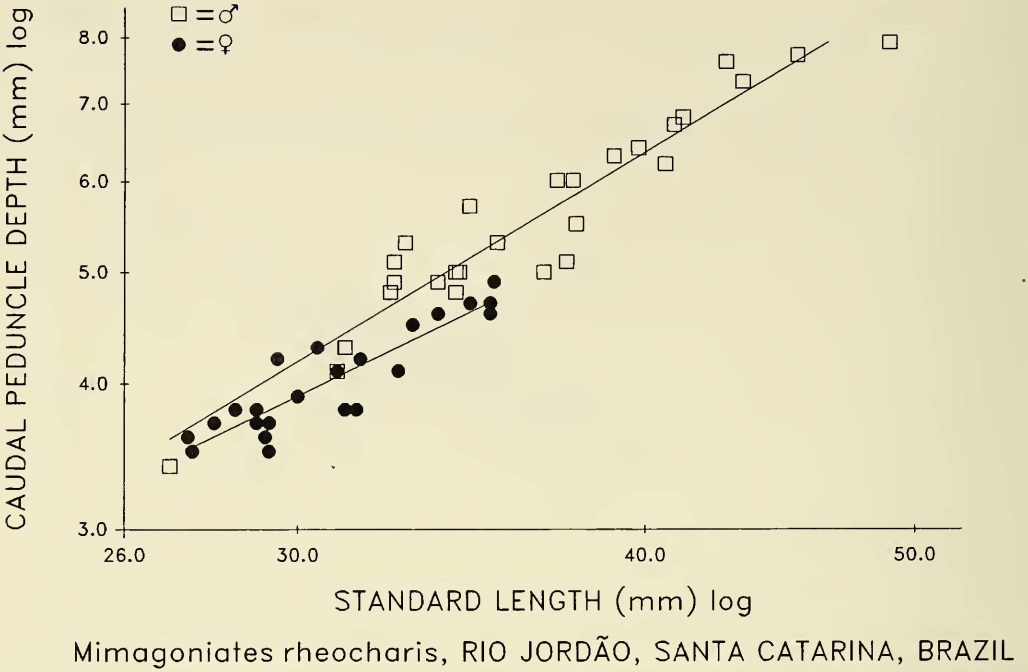

Fig. 28. *Mimagoniates rheocharis,* new species, paratypes caudal peduncle depth as a function of SL by sex. Plot axes are logarithmic. Logarithmic regression equation for 27 males of *M. rheocharis*: (Y = −3.490 + 1.447X) and for 23 females of *M. rheocharis*: (Y = −2.606 + 1.167X). For explanation see Sexual dimorphism under *M. rheocharis.*

mone organ. Rays 17–19 (ventral caudal-fin lobe) hyaline or nearly hyaline except ray 17 which is somewhat yellow. Remainder of black pigment of caudal fin as described above for preserved specimens.

Anal fin with distal portion of fin rays posterior to anterior anal-fin lobe lemon yellow, forming a stripe along ventral border of fin. Distal region of anterior anal-fin lobe hyaline to white, proximally bordered by black pigment described above for preserved specimens. This black pigment mixed with yellow. Basal half of anal fin hyaline with some scattered brown chromatophores and a small amount of yellow anteriorly. Posterior portion of narrow horizontal black line of anal fin pale. Approximately distal half of pelvic fin white; a black and yellow band proximal to this; remaining proximal portion of fin hyaline. Distal half of pectoral fins yellow, proximal half with black rays and yellow membranes. Dorsal fin hyaline to white distal and proximal to longitudinal black and brown longitudinal stripe.

Sexual dimorphism.—Females lack a caudal pheromone pump organ and pelvic-fin and anal-fin hooks described above for males. Live color of females is unknown but undoubtedly more subdued than that of sexually mature males. Figure 17 graphically indicates that according to these population samples, males and females of *M. rheocharis* and *M. microlepis* respectively show no significant sexual dimorphism in body depth. In an *F*-ratio test for homogeneity of slopes in an analysis of covariance for body depth on SL of *M. rheocharis,* no significant difference was found for 31 males and 25 females from Praia Grande (MZUSP 40270, 40280, MCP 13616, and USNM 279878, 306339. The above sample included very young as well as fully adult speci-

Table 2. Morphometrics of *Mimagoniates rheocharis*, new species. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Specimens are from near Rio Grande, Santa Catarina, MZUSP 40278, 40280, MCP 13616, and USNM 279878, 306339.

	Holotype	n	Range	$\bar{x}$
Standard length	47.3	57	13.5–47.8	29.5
Depth at dorsal-fin origin	—	57	22.2–35.2	30.5
Males	33.8	31	26.9–35.2	31.4
Females	—	26	22.2–32.9	29.4
Snout to dorsal-fin origin	57.9	57	54.6–60.7	58.0
Snout to pectoral-fin origin	26.6	57	24.2–29.6	26.3
Snout to pelvic-fin origin	43.4	57	40.4–47.6	45.0
Snout to anal-fin origin	58.8	57	52.3–58.8	56.9
Caudal peduncle depth	—	57	8.9–16.3	13.4
Males	16.0	31	11.5–16.3	14.2
Females	—	26	8.9–14.2	12.4
Caudal peduncle length	11.4	57	7.1–13.3	9.9
Pectoral-fin length	21.6	57	18.5–24.9	22.7
Pelvic-fin length	12.3	57	11.1–15.1	13.4
Dorsal-fin base length	17.3	57	12.7–19.1	15.8
Dorsal-fin height	26.0	57	20.7–28.0	23.7
Anal-fin base length	34.5	57	33.7–38.7	36.0
Anal-fin lobe length	19.0	57	15.6–22.6	19.9
Eye to dorsal-fin origin	45.9	57	41.5–48.3	45.2
Dorsal-fin origin to caudal-fin base	46.5	57	39.3–49.2	45.4
Bony head length	25.6	57	24.2–28.1	25.5
Horizontal eye diameter	33.1	56	33.1–48.1	39.5
Snout length	24.8	56	20.0–26.2	22.5
Least interorbital width	33.9	56	28.9–40.4	36.0
Upper jaw length	43.8	56	42.9–50.0	45.7

mens. Juveniles of undetermined sex were entered as females since young females are indistinguishable from juveniles in body depth.

In another sample of *M. rheocharis* consisting of only adults from rio Jordão (MZUSP 40279, MCP 13617 and USNM 279879), Fig. 25, the same statistical test for body depth as a function of SL in 27 males and 23 females demonstrated no significant difference between slopes but does show a significant difference ($F_{0.05,\ (1,\ 47)} = 18.67$, $P < 0.001$) in adjusted means. Both Figs. 25 and 26 indicate considerable sexual dimorphism in body length for *M. rheocharis.*

Figures 27 and 28 provide graphic evidence that there appears to be a divergence in caudal peduncle depth between males and females of *M. rheocharis* as they become sexually mature and increase in length. We have few females over 33.0 mm in SL so the nature of caudal peduncle depth divergence between males and females remains unsampled if females reach the same SL as males. We doubt that happens, because in all the population samples of various species of *Mimagoniates* examined by us, the males reach a greater adult length than females. Thus, again in our analyses of sexual dimorphism our comparison of males and females of unequal body lengths is probably an expression of reality rather than of missing data for females. In *F*-ratio tests of an analysis of covariance for caudal peduncle depth on SL, no significant difference was found for the homogeneity of slopes between 30 male specimens and 25 females although a significant difference ($F_{0.05,(1,52)} = 22.33$, $P < 0.001$) in adjusted means was evident; see also Fig. 27. This population sample is from the specimens reported above from near Praia Grande. In another population sample, the same one reported above regarding body depth as a function of SL from rio Jordão, the slopes of the females versus males were not significantly different in caudal peduncle depth as a function of SL (Fig. 28) but the adjusted means are significantly different ($F_{0.05,(1,47)} = 18.67$, $P < 0.001$) and are similar to those reported above from near Praia Grande rio Grande region, Santa Catarina.

Statistical comparisons.—As noted in the Diagnosis above and the Discussion below of *M. rheocharis,* comparisons testing hypotheses of significant statistical difference between *M. rheocharis* and two species, *M. microlepis* and *M. inequalis,* were necessary because many of their characters overlap and because of the need to examine, in a preliminary way, the possibilities of introgression among these species.

Body depth as a function of SL in an *F*-ratio test for homogeneity of slopes (Fig. 17) showed no significant differences in an analysis of covariance between 31 males of *M. rheocharis* from rio Grande region, Santa Catarina (MZUSP 40280, USNM 306339) and 39 males of *M. microlepis* from the area near Paranaguá, Paraná (MZUSP 40288, USNM 306378) but did show a significant difference ($F_{0.05,(1,67)} = 188.05$, $P < 0.000$) in adjusted means. Same analysis for 24 and 31 females respectively from same localities also showed no significant difference in slopes but did show such a difference ($F_{0.05,(1,53)} = 82.97$, $P < 0.000$) in adjusted means.

Caudal peduncle depth as a function of SL in an *F*-ratio test for homogeneity of slopes (Fig. 27) showed no statistically significant difference in an analysis of covariance between 30 males of *M. rheocharis* from near Praia Grande, rio Grande region, Santa Catarina (MZUSP 40280, USNM 306339) and 40 males of *M. microlepis* from area near Paranaguá, Paraná (MZUSP 40288, USNM 306378) but did show a significant difference ($F_{0.05,(1,67)} = 94.36$, $P = 0.000$) in adjusted means. Same analysis for 26 and 31 females respectively from same localities also showed no significant differences in slopes but did show such a difference ($F_{0.05,(1,54)} = 106.03$, $P < 0.000$) in adjusted means.

Number of scale rows between dorsal-fin origin and anal-fin origin of *M. rheocharis* (17–22) and *M. microlepis* (14–17) overlaps somewhat but is statistically significantly different. Forty-two specimens of *M. rheocharis* ($\bar{x}$ = 19.6, range = 18–22, SD = 0.8211) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 58 specimens of *M. microlepis* ($\bar{x}$ = 15.2, range = 14–17, SD 0.6702) do not overlap but 53 specimens of *M. rheocharis* ($\bar{x}$ = 18.8, range = 17–21, SD = 0.8905) from the rio Grande region of Santa Catarina do overlap with the specimens of *M. microlepis* just noted. These last two samples are significantly different ($t = 24.959$, $P = 0.00$).

Lateral series scale counts, as noted above broadly overlap but one case of 48 specimens of *M. rheocharis* ($\bar{x}$ = 44.2, range = 41–48, SD = 1.7704) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 45 specimens of *M. microlepis* ($\bar{x}$ = 45.0, range = 42–49, SD = 1.5948) from Paranaguá and rio Nhundiaquara (MZUSP 40281, USNM 249886, 249890, 249894, 249897, 257114, 257115, 257198) showed a significant difference ($t = 2.459$, $P = 0.015$).

Branched dorsal-fin ray count higher (8–12, $\bar{x}$ = 9.4) for *M. rheocharis* than any other species in tribe Glandulocaudini (branched dorsal-fin rays almost always 8, rarely 7 or 9) and constitutes an autapomorphy for the species. Two sampled populations differed considerably from one another in this count. Fifty specimens of *M. rheocharis* ($\bar{x}$ = 9.8, range = 9–12, SD = 0.6701) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879 and 56 specimens of this species ($\bar{x}$

= 8.9, range = 8–10, SD = 0.4615) from rio Grande region of Santa Catarina (MZUSP 40280, USNM 306339) were significantly different ($t = 7.901$, $P = 0.00$). Both of these population samples of *M. rheocharis* differed significantly from that of 70 specimens of *M. microlepis* ($\bar{x} = 8.0$, range = 7–9, SD = 0.1703) from area near Paranaguá and rio Nhundiaquara, Paraná (MZUSP 40281, 40288, USNM 249886, 249890, 249894, 24897, 257114, 257115, 257198, 306378). Thus, $t = 22.490$, $P = 0.00$ for rio Jordão sample and $t = 9.472$, $P = 0.00$ for rio Grande sample of *M. rheocharis.*

Branched anal-fin ray counts, although overlapping for these two species are statistically different ($t = 19.402$, $P = 0.00$) in 50 specimens of *M. rheocharis* ($\bar{x} = 25.3$, range = 23–27, SD = 1.1073) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 70 specimens of *M. microlepis* ($\bar{x} = 29.7$, range = 26–33, SD = 1.2471) from near Paranaguá and rio Nhundiaquara at Morretes, Paraná, (MZUSP 40281, 40288, USNM 306378, 249886, 249890, 249894, 249897, 257114, 257115). A second population sample of 56 specimens of *M. rheocharis* ($\bar{x} = 26.8$, range = 25–29, SD = 1.3088) from area of rio Grande, Santa Catarina (MZUSP 40278, 40280, MCP 13616, USNM 279878, 306339) also differed significantly in a similar test from the Paranaguá and rio Nhundiaquara samples ($t = 12.1510$, $P = 0.00$).

Vertebral counts of *M. rheocharis* and *M. microlepis* overlap somewhat, but they are significantly different ($t = 12.528$, $P < 0.00$): $\bar{x} = 38.0$, range = 37–40, SD = 0.6558, $n = 87$ for *M. rheocharis* from rio Jordão (MZUSP 40279, USNM 270879) and $\bar{x} = 39.3$, range = 38–41, SD = 0.6532, $n = 70$ for *M. microlepis* from rio Nhundiaquara (MZUSP 40281, USNM 249886, 249890, 249894, 249897, 257114, 257115, and 257198).

In the following statistical comparisons of *M. rheocharis* and *M. inequalis,* specimens of the latter species from an arroio near Morungava, Município de Gravataí, Rio Grande do Sul (MAPA 115), were chosen for comparison because they came from the rio Gravataí system, a drainage adjacent to the streams around Osório which contain *M. rheocharis.* See also in the *Discussion* below comparison of our few specimens of *M. rheocharis* from the adjacent streams around Osório and the rio Maquiné just to the north of Osório.

Body depth as a function of SL in an F-ratio test for homogeneity of slopes (Fig. 17) showed no significant difference in an analysis of covariance between 31 males of *M. rheocharis* from rio Grande region, Santa Catarina (MZUSP 40280, USNM 306339) and 26 males of *M. inequalis* from Morungava, Rio Grande do Sul (MAPA 115) but did show a difference ($F_{0.05,(1,54)} = 50.03$, $P < 0.000$) in adjusted means. Same analysis for 25 females and 14 females of each species respectively from same localities showed a significant difference ($F_{0.05,(1,36)} = 42.41$, $P < 0.000$) in body depth on SL only for adjusted means.

Caudal peduncle depth as a function of SL in an F-ratio test for homogeneity of slopes (Fig. 27) showed no statistically significant difference in an analysis of covariance between 30 males of *M. rheocharis* from rio Grande, Santa Catarina (MZUSP 40280, USNM 306339) and 26 males of *M. inequalis* from Morungava, Rio Grande do Sul (MAPA 115) but did show a significant difference ($F_{0.05\,(1,53)} = 43.95$, $P < 0.000$) in adjusted means. Some test for 26 females and 14 females respectively from same localities showed a significant difference ($F_{0.05,(1,37)} = 69.18$, $P < 0.000$) only in adjusted means.

Number of scale rows around caudal peduncle of *M. rheocharis* (19–22) and *M. inequalis* (16–19) overlaps slightly but is significantly different. No overlap for present 17 specimens of *M. rheocharis* ($\bar{x} = 21.5$, range = 20–22, SD = 0.7174) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 34 specimens of *M. inequalis*

($\bar{x}$ = 17.6, range 16–19, SD = 0.8170) from Morungava, Rio Grande do Sul (MAPA 115). Number of scale rows around caudal peduncle overlaps slightly in 46 specimens of *M. rheocharis* ($\bar{x}$ = 19.7, range = 19–22, SD = 0.7520) from rio Grande region of Santa Catarina (MZUSP 40280, USNM 306339) and those just listed just above of *M. inequalis,* but counts significantly different ($t = 12.011$, $P = 0.00$).

Number of scale rows between dorsal-fin origin and anal-fin origin of *M. rheocharis* (17–22) and *M. inequalis* (16–18) also overlaps somewhat but again is statistically significantly different. There is an overlap in 42 specimens of *M. rheocharis* ($\bar{x}$ = 19.6, range = 18–22, SD = 0.8211) from the rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 40 specimens of *M. inequalis* ($\bar{x}$ = 16.5, range = 16–18, SD = 0.6405) from Morungava, Rio Grande do Sul (MAPA 115), but these counts are significantly different ($t = 19.565$, $P = 0.00$).

Lateral series scale count of *M. rheocharis* (41–48) and *M. inequalis* (36–41) overlaps somewhat but is significantly different statistically. No overlap occurs in 26 specimens of *M. rheocharis* ($\bar{x}$ = 45.5, range = 43–48, SD = 1.4760) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 38 specimens of *M. inequalis* ($\bar{x}$ = 38.3, range = 36–41, SD = 1.1455) from Morungava, Rio Grande do Sul (MAPA 115). Lateral series scale count overlaps slightly in 48 specimens of *M. rheocharis* ($\bar{x}$ = 44.2, range = 41–48, SD = 1.7704) from rio Grande region of Santa Catarina (MZUSP 40280, USNM 306339) and those just listed of *M. inequalis,* but these counts are significantly different ($t = 17.922$, $P = 0.00$).

Branched dorsal-fin ray count in 50 specimens of *M. rheocharis* ($\bar{x}$ = 9.8, range = 9–12, SD = 0.6701) from rio Jordão (MZUSP 40279, USNM 270879) differed significantly from a sample of 40 specimens of *M. inequalis* ($\bar{x}$ = 8.125, range = 8–9, SD = 0.3349) from Morungava, Rio Grande do Sul (MAPA 115) ($t = 14.951$, $P = 0.00$). Same comparison for 56 specimens of *M. rheocharis* ($\bar{x}$ = 8.9, range = 8–10, SD = 0.4615) with same sample of *M. inequalis* just mentioned was also significantly different ($t = 9.472$, $P = 0.00$).

Branched anal-fin ray counts overlap for both species but are statistically significantly different ($t = 6.336$, $P = 0.00$) in 50 specimens of *M. rheocharis* ($\bar{x}$ = 25.3, range = 23–27, SD = 1.2471) from rio Jordão (MZUSP 40279, MCP 13617, USNM 270879) and 40 specimens of *M. inequalis* ($\bar{x}$ = 26.7, range = 24–30, SD = 0.9443) from Morungava, Rio Grande do Sul (MAPA 115). These not significantly different in a second population sample of 56 specimens of *M. rheocharis* ($\bar{x}$ = 26.8, range = 25–29, SD = 1.3088) from rio Grande, Santa Catarina (MZUSP 40278, 40280, MCP 13616, USNM 279878, 306339) from that of *M. inequalis* just described.

Vertebral counts, $\bar{x}$ = 38.0, range = 37–40, SD = 0.6558, $n = 87$, for *M. rheocharis* from rio Jordão (MZUSP 40279, USNM 27879) and, $\bar{x}$ = 37.9, range = 36–39, SD = 0.7055, $n = 70$, for *M. inequalis* from Morungava, Rio Grande do Sul (MAPA 115) are not significantly different statistically.

Etymology.—The name *rheocharis* is from the Greek *rheos* (= current or stream) and *charis,* also Greek, (= loveliness, grace or charming) and is in reference to the streams in which this fish has been taken and to the beauty of the fish itself.

Discussion.—The phylogenetic relationships of *M. rheocharis* are uncertain but fully mature males, as noted above, have a caudal fin-ray pump chamber, a putative synapomorphy uniting that species with *M. sylvicola, M. lateralis,* and *M. microlepis. Mimagoniates inequalis* and *M. barberi* are not included in this group because they lack a caudal pump chamber, having only a groove in its place.

Weitzman et al. (1988:412) tentatively hypothesized that *M. rheocharis,* as new species B, is a sister species of *M. microlepis* because these species share caudal-fin hooks (absent in other species of *Mimagoniates*) distal to the pump area on principal caudal-fin rays 10 and 11. These hooks are not nearly as numerous or as large in *M. rheocharis* as they are in *M. microlepis* (compare Figs. 5 and 24). We found no other synapomorphy uniting these two species. *Mimagoniates rheocharis* and *M. microlepis* thus may still be hypothesized as one another's closest relatives (Fig. 1). However, Fig. 1 is presented primarily as a visual aid to the discussion that follows. We accept the hypothesis it presents with reservations because the relationships of *M. rheocharis* may be quite complex due to a possible hybrid origin or at least some introgression with other species. Furthermore a considerable amount of character conflict exists among all the species of *Mimagoniates* making acceptance of many of the relationships suggested in Fig. 1 quite questionable.

A number of differences, outlined in the key and diagnosis above, were found among *M. rheocharis* and *M. microlepis* and *M. inequalis.* Although these differences indicate these species are divergent, many of these characters cannot at present be used to corroborate hypotheses of phylogenetic relationship with other species of *Mimagoniates* because so far they have not been identified as synapomorphies shared among other species. Certain of these characters are continuously variable between at least some species, for example between *M. rheocharis* and *M. inequalis,* possibly limiting their use as characters suitable for phylogenetic analyses, Chappill (1989) and Pimentel & Riggins (1987). Some of the states of these characters as shared by *M. rheocharis* and *M. inequalis* are plesiomorphic with respect to their condition in other species of *Mimagoniates,* making their use as synapomorphies for these two species impossible. For example, outgroup comparison with species of *Glandulocauda* and species in other tribes of the Glandulocaudinae indicates that relatively short overall body shape and central median fin position of *M. rheocharis,* shared with *M. inequalis,* is plesiomorphic with respect to the more elongate body and posterior dorsal-fin position in *M. microlepis, M. lateralis, M. sylvicola* and *M. barberi* (see also comments below). Relatively elongate body shapes might be considered synapomorphic for the latter four species but use of this character for corroboration of phylogenetic hypotheses in the Glandulocaudini is still in need of further study and may be difficult to use at some nodes because of continuous variability. The high number of dorsal-fin rays (8–12 in *M. rheocharis* versus 7–9 in other species of *Mimagoniates*) appears autapomorphic for that species, but, again the character is continuously variable between *M. inequalis, M. rheocharis* and other species of *Mimagoniates.*

If these and other similar characters can be used as synapomorphies at some nodes, then character conflict and complex homoplasies will need to be resolved using parsimony with enough corroborated evidence to be convincing. For example, at present at least three characters or character complexes appear in conflict with one another in regard to their possible significance in suggesting phylogenetic relationships. These are relative body length, relative derivation of the caudal pump and the presence or absence of a prominent lateral mid-side dark stripe. For example, if elongate body, present in *M. sylvicola, M. lateralis, M. barberi* and *M. microlepis,* were hypothesized to have evolved only once then these four species would form a monophyletic line based on this character. Then the caudal fin-ray pump chamber might have evolved twice, once in *M. rheocharis* and again in a clade including *M. lateralis, M. sylvicola* and *M. microlepis.* On the other hand, monophyly based in part on elongate body could result in a phylogeny wherein *M. lateralis* was the sister species to all of the other species just mentioned and *M. rheocharis* regained a relatively short body shape.

Again, *M. lateralis* and *M. barberi* share the possession of a dark brown or black broad lateral stripe extending from the lower jaw tip posteriorly across the body sides to the region of the caudal gland on the caudal fin. A hypothesis that considers this character synapomorphic for these two species requires that the pump chamber evolved more than once, independently in *M. lateralis,* and in a clade consisting of *M. sylvicola, M. rheocharis* and *M. microlepis,* a phylogenetic configuration different from those noted above for acceptance of elongate body as a synapomorphy for four species of *Mimagoniates.* Finally, if one hypothesizes that a fully derived caudal fin-ray pump chamber evolved only once in a clade consisting of *M. sylvicola, M. lateralis, M. rheocharis* and *M. microlepis,* then both the lateral stripe and elongate body would have evolved twice each and in a phylogenetic configuration different from any of those above. At this time the above speculations and others like them are fruitless and we mention them only to point out the current complexities regarding the phylogeny of the species of *Mimagoniates.* As yet we have not fully investigated the possible phylogenetic significance of many of the characters putatively available for phylogenetic analysis of the Glandulocaudini. The matter is quite complex and the use of parsimony to propose acceptable phylogenetic hypothesis and resolve the problems of character polarities will naturally still result in numerous homoplasies. We might add that the use of any "method" other than parsimony to resolve character conflict will not eliminate all homoplasies but only subjectively delete some rather than others.

As noted above, we tentatively hypothesize that *M. rheocharis* and *M. microlepis* are sister species based on fin-ray secondary sexual characters which do not appear to be continuously variable and may be synapomorphic if the character conflicts mentioned above can be resolved in a form that favors the secondary sexual fin-ray structures. However, as one might expect, there are complications and possible alternative hypotheses of phylogenetic relationships other than those mentioned above. For various reasons some of these should be briefly discussed.

In searching for possible alternate hypotheses of phylogenetic relationship for *M. rheocharis* we note that this species and *M. inequalis* look remarkably alike in general body shape, fin position, body color and the counts recorded above as separating the species are not remarkably different. Both species lack the distinct mid-lateral body stripe found in *M. lateralis* and *M. barberi.* Furthermore, both species have closely similar vertebral counts that are not significantly different, $n = 39$ for specimens of *M. inequalis* from Arroio Fiuza near Passo Fiuza, Municipio de Viamão, south east of Porto Alegre, Rio Grande do Sul, (USNM 254273), $\bar{x} = 38.0$, range = 35–39, SD = 0.6489 and $n = 87$ for specimens of *M. rheocharis* from rio Jordão, (MZUSP 40279, USNM 279879), $\bar{x} = 38.0$, range = 37–40, SD = 0.6288. See also the nearly identical results of a different comparison of vertebral numbers and other counts given in the section labeled Statistical Comparisons. These vertebral counts are relatively low when compared with those of the more elongate species of *Mimagoniates* such as *M. rheocharis* but broad overlap occurs, again see section above labeled *Statistical Comparisons,* and we are unable to show that shared vertebral counts by *M. rheocharis* and *M. inequalis* are shared derived characters. We discuss such characters only to point out the difficulties in attempting to study the relationships of the species of *Mimagoniates* based on characters other than those directly associated with their secondary sexual characteristics.

Our preliminary analysis suggests that these character similarities are unlikely to be synapomorphic for *M. rheocharis* and *M. inequalis* because these features are also found in immediate outgroups down the tree, for example species of *Glandulocauda* and certain of the apparently less derived glandulocaudine species belonging to tribes that are possibly sister groups to the Glandulocaudini. However, our analysis is incomplete and alternate hypotheses suggesting that *M. inequalis* and *M. rheocharis* are sister species or related in some way cannot be confidently rejected at this time.

The intermediacy of the *M. rheocharis* between *M. inequalis* and *M. microlepis* in body depth and caudal peduncle depth (Figs. 17, 27) was noted above in the Diagnosis and the Statistical Comparison section of *M. rheocharis.* The relatively modest development of the fin-ray pump chamber and of the small and few caudal-fin spines on rays 10 and 11 in *M. rheocharis,* rather than being considered plesiomorphic relative to the state of these structures in *M. microlepis,* could be considered intermediate between the state in *M. inequalis* (no spines, no pump chamber) and that in *M. microlepis* (many well developed spines, and a highly developed fin-ray pump chamber). This suggests a possible origin of *M. rheocharis* by introgression between *M. microlepis* and *M. inequalis.* However, a hypothesis of hybrid origin for *M. rheocharis* might be rejected because it does have autapomorphies that are absent in both *M. inequalis* and *M. microlepis.* Even then, it cannot be discounted that *M. rheocharis* might have originated through introgression in a geographical range once shared by the ancestors of the current populations of *M. inequalis* and *M. microlepis* and that the autapomorphies of *M. rheocharis* evolved subsequent to that introgression at a time when *M. rheocharis* became isolated from its parent populations. The current geographical ranges of these species would be congruent with such a biogeographical hypothesis but in our view this hypothesis, just as any hypothesis of species origin by introgression, unless corroborated by genetic data as well as much statistical data on morphology from pertinent natural populations, is less parsimonious than that of sister status, in this case between *M. rheocharis* and *M. microlepis.* Because we lack such data, we currently reject this introgression hypothesis. If *M. rheocharis* did evolve in part through introgression, according to our hypotheses of phylogeny among the species of *Mimagoniates* this introgression would have taken place between two of the more distantly related members of the genus, something we view as possible but in need of study by breeding experiments and intensive statistical analyses of the characters of the three species from population samples in the areas of their contingency and sympatry.

It might be proposed that specimens of *M. rheocharis* are simply hybrid individuals between *M. inequalis* and *M. microlepis* but several factors argue against this. First, only one of the putative parent species occurs in the present range of *M. rheocharis,* that is *M. microlepis* which is sympatric and syntopic with *M. rheocharis. Mimagoniates inequalis,* as explained above, is so far as known allopatric with *M. rheocharis,* preventing it from being a parent of current specimens of *M. rheocharis.* Furthermore, *M. rheocharis* has autapomorphic characters not present in either putative parent.

Another hypothesis of phylogenetic relationship, one that is less parsimonious than sister species status for *M. rheocharis* and *M. microlepis,* could be put forward and we mention this one only because of its implications regarding the dangerous practice of assuming biogeographical significance for geographically adjacent similar looking species, done by some biogeographers. One could hypothesize that *M. rheocharis* and *M. inequalis* are sister species. This hypothesis is not out of the realm of possibility even though current character polarity hypotheses for secondary sexual characters indicate that other features shared by these latter two species are plesiomorphic at this level of relationship. Nevertheless, if such a hypothesis were true the current distributions of these two species would make good historical biogeographical sense. *Mimagoniates inequalis* is found in the freshwater biogeographical South Coastal Subregion of Menezes (1988:300) and *M. rheocharis* is found in the adjacent southern part of his Central Coastal Subregion. A simple vicariance or dispersion event historically separating two parts of an ancestral population for the two species could have been responsible for initiating their evolution. However, the phylogenetic evidence, in all its current uncertain status, does not support such a hypothesis of phylogeny and therefore does not support this historical biogeographical pattern. This example provides one reason why we refuse to use current distributional patterns of species as either evidence of relationships among organisms or as direct indicators of historical biogeographic events. Most distribution patterns may correlate with a variety of phylogenetic and biogeographic scenarios and cannot be used as primary evidence for any given one.

Another problem with some of our data remains to be discussed. Given the current limitations of our population samples and the small adult lengths of most of our specimens of *M. inequalis,* it is difficult to place too much confidence in certain aspects of the above phylogenetic discussions based on some secondary sexual characteristics. This is true because at least one, caudal pump morphology, of the phylogenetically important characters currently available for *M. rheocharis* and its possible relatives such as *M. inequalis,* is based on a character that may be juvenile, that is not representing a character state attained in fully mature adults of that species. Such juvenile character states may then be compared incorrectly with homologous but fully adult characters in another species, leading to invalid conclusions regarding the relative apomorphy of these characters. This kind of problem affects both of the very separate tasks of studying phylogenetic relationships and of distinguishing species from one another, witness our caution about couplet four in our key above and our mistake in Weitzman et al. (1988) regarding the relative apomorphy of the caudal gland in *M. sylvicola* (see the Discussion above of that species). Regarding *M. inequalis* in the current treatment, perhaps our collections contain no fully adult males of this species and at the completion of sexual maturity, males have a caudal fin-ray pump chamber similar to that found in males of *M. rheocharis.* If this were true the phylogenetic relationships we have presented based on caudal morphology would be drastically altered. The evidence we have bearing on this problem is as follows. A male specimen of each of the two species of nearly equal length (one, *M. inequalis,* SL 38.8 mm, MCP 9892, from rio Caí drainage, Rio Grande do Sul, and the other, *M. rheocharis,* SL 39.5 mm, MCP 10806, from rio Três Furquilhas, Rio Grande do Sul), indicate that *M. rheocharis* has a well-developed caudal-fin ray pump chamber as well as tiny hooks on principal caudal fin-rays 10 and 11 and that *M. inequalis* only has a groove and no hooks. Also, two old aquarium specimens of male *M. inequalis* (USNM 94310, originally imported from Porto Alegre and grown to "old age" in an aquarium by Herman Meinken) have standard lengths of 38.2 and 41.0 mm. The latter specimen is the largest we have of this species. These specimens show no evidence of a caudal pump chamber or hooks on fin-rays 10 and 11 but do have a groove. Furthermore, three smaller (SL 28.5–31.3 mm) sexually mature males of *M. rheocharis* (MCP 13613, from arroio Água Parada, a tributary of the rio Maquiné from near Maquiné, Rio Grande do Sul) have well-developed pump chambers as well as tiny hooks present on caudal-fin rays 10 and 11. These facts reinforce our hypothesis that *M. rheocharis* is a derived species distinct from the more plesiomorphic *M. inequalis.*

The specimens of *M. rheocharis,* MCP 13613, three males and four females, from arroio Água Parada plus a single large specimen (SL 41.8 mm, MZUSP 40281, Fig. 20, from a nearby locality, arroio das Pedras near Osório), are interesting in light of the introgression hypotheses discussed above. The meristic characters that help distinguish *M. inequalis* and *M. rheocharis* are all within the overlapping range of the two species (9 branched dorsal-fin rays, 16–17 scale rows between the dorsal-fin and anal-fin origins, 18–19 scale rows around the caudal peduncle and 42–43 scales in a lateral series). Although these counts fall well within the range of those of other population samples of *M. rheocharis* to the north, they do fall closer to those counts of *M. inequalis* than any of our other population samples of *M. rheocharis*. Compare the counts just given with those presented in the comparative section of the Diagnosis of *M. rheocharis* above. We also note that these localities for *M. rheocharis* near Osório lie adjacent to the rio Gravataí drainage just to the west which is occupied by *M. inequalis*. We are unsure of the real significance of these counts but they could imply some gene flow between *M. rheocharis* and *M. inequalis* in this region at some time in the past. We are unaware of any current sympatry of these two species in this region but the area is not well sampled.

In summary, the phylogenetic relationships of *M. rheocharis* are uncertain. It could simply be a sister species of *M. microlepis* with a somewhat more plesiomorphic state of the caudal pheromone origin, a somewhat derived sister species of *M. inequalis*, a species derived by introgression between *M. inequalis* and *M. microlepis* with subsequent evolution of some autapomorphic characters, or, for example, a sister species of *M. microlepis* which may be introgressing with *M. inequalis*. Other hypotheses of phylogenetic relationship could be suggested but these examples are sufficient to indicate the possible complexities of the phylogeny of *M. rheocharis*. Because the shared characters of *M. rheocharis* and *M. inequalis* have been hypothesized to be pleisomorphies in the context of the entire phylogeny of the Glandulocaudini, we, at least for now, accept the evidence that the male caudal secondary sexual characters represent synapomorphies and tentatively propose sister species status for *M. rheocharis* and *M. microlepis*. The other hypotheses of possible phylogenetic relationship await considerable additional evidence for possible corroboration.

Ecology.—We do not have extensive notes on the ecology of this species but the following information is taken from notes by Carlos Lucena from two localities (one the type locality) and by Ricardo M. C. Castro from two localities.

Specimens collected by C. A. S. de Lucena and party from rio Faxinalzinho at Mãe dos Homens, rio Mampituba drainage, near Praia Grande, the type locality, MZUSP 40278, MCP 3616, USNM 279878, were removed from a clear-water stream 2–6 m wide, 0.1–1.0 m deep, with a moderate current. There was a moderate amount of (unspecified) marginal vegetation present. The substrate consisted of rubble, rocks, stones, and gravel. *Mimagoniates microlepis* and a species of each of *Rhamdia, Rhamdella, Heptapturus, Ancistrus, Rhineloricaria, Pseudotocinclus, Pareiorhyna, Corymbophanes, Trichomycterus, Characidum,* an unspecified species of tetragonopterine characid, two species of *Astyanax,* and a species of *Jenynsia* were present.

The second locality collected by Carlos Lucena and party was rio Jordão near Jordão Alto, MCP 13617, MZUSP 40279, and USNM 270879. This was the upper region of the rio Jordão where the stream was 1–5 m wide and 0.1–0.7 m deep. The current was slow, there was a small amount of (unspecified) marginal vegetation, and the substrate consisted of rubble, rocks, stones, gravel, sand and mud. The fishes that were collected at the same locality were species of *Rhamdia, Heptapterus, Ancistrus,* two loricariids unidentified to genus, *Rhineloricaria, Pseudotocinclus,* two species of *Tri-*

chomycterus, Characidium, Hoplias, Astyanax, an unidentified tetragonopterine characid, *Phalloceros, Jenynsia, Geophagus brasiliensis* and *Cichlasoma facetum.*

The first locality collected by Ricardo Castro is from near Osório, Rio Grande do Sul, MZUSP 40281. The specimen was collected in a small clear-water stream about 1.5 m wide and 20 cm deep, surrounded by shrubs and small trees. The water was clear, with very little suspended matter. Algae covered rocks were common on the substrate. Other fishes collected in the area were species of *Astyanax, Oligosarcus, Rhamdia,* and a small unidentified catfish.

Specimens of *M. rheocharis* from a tributary of the rio Grande, Santa Catarina, MZUSP 40280 and USNM 306339, were collected from a slow moving clear water stream about 1.5 m wide and 30 cm deep. Not far away the stream flowed into the larger river. Rocks, sand, soil and twigs fallen from nearby trees were the main substrate components. The rocks and twigs were densely covered with algae. The stream was bordered by rocks, mud, grass and small trees in many places.

Biogeography

Weitzman et al. (1988:404) tentatively hypothesized that *M. inequalis, M. barberi* and *M. sylvicola* (as new species A) were less derived than the remaining species of *Mimagoniates* and that they might form a natural group although the three species shared no synapomorphies. This hypothesis was used to make the statement that species with a relatively primitive pump morphology are distributed peripheral to the other, more derived species. The evolution of those species with derived caudal pumps was hypothesized to have taken place where they now live, the central area of the north to south coastal stream distribution of *Mimagoniates,* roughly from southern Bahia to northern Rio Grande do Sul. We suggested that at one time a species of *Mimagoniates* with a relatively simple, primitive caudal-fin pheromone pump may have been distributed throughout the current range of *Mimagoniates* and that subsequent vicariance and/or dispersion events associated with changes in sea level may have played a major role in speciation and the evolution of the complex fin-ray pump. Evidence for dispersion by stream capture or other means of migration was considered because some of the species were found to be in part or wholly sympatric (in some cases allotopic and in others syntopic). Weitzman et al. (1988:414) also hypothesized that the most derived species, *M. microlepis,* distributed in coastal stream from southern Bahia to northern Rio Grande do Sul, reached the upper rio Iguaçu drainage by stream capture or possibly was introduced by man.

As indicated above in the present Discussion of *M. sylvicola,* this species has a well-developed caudal pump chamber and therefore there is no direct evidence that a primitive species ever existed at the northern end of the current known range of the species of *Mimagoniates.* This does not mean that one never existed there, since it could have been replaced by the more derived species currently in that location, a hypothesis only testable by fossil evidence. If the phylogenetic relationships hypothesized here for *M. sylvicola* are correct, we might assume that caudal pump chamber evolution took place throughout the coastal stream distribution of *Mimagoniates* in Brazil north of the current distribution of *M. inequalis* in the state of Rio Grande do Sul.

If the phylogenetic hypothesis that *M. rheocharis* and *M. microlepis* are sister species can be accepted, then at one time in the past a vicariance or perhaps a dispersion event isolated two populations of the parent species, possibly in or at least near the current range of *M. rheocharis.* Subsequently further evolution of the caudal organ took place in *M. microlepis.* It would appear that subsequent dispersion of *M. microlepis* into the range of *M. rheocharis* resulting in their present sympatry is the at least one likely scenario but the reverse could also be true at least in part. Speculations about patterns of dispersion other than the mention of their existence are often sterile because data bearing directly on the problem are limited to fossil evidence. If any one of the alternate hypotheses of introgression or sister species relationship with *M. inequalis* for *M. rheocharis* represent reality, it would alter the above biogeographical hypothesis. However, currently there is no reason to discuss such an alteration beyond a brief mention of its possibility. See also the comments concerning biogeography in the Discussion above on the relationships of *M. rheocharis,* especially those on the possible sister species status between *M. rheocharis* and *M. inequalis.*

The problem of speciation as it bears on the biogeography of *Mimagoniates* is quite complex because ecological adaptations, climatic and geomorphological change in association with either vicariance, dispersion, and/or introgression may have played major roles in the evolution of some its species. See especially our comments above regarding introgression and sister species status in the Discussion above of *M. rheocharis.* The biogeographical problems associated with ecological adaptations in species of *Mimagoniates* are little understood but we have enough information to indicate that they cannot be ignored.

For example, of the two species hypothesized above to be sister species, the distribution of *M. rheocharis* is sympatric with that of *M. microlepis.* The information we have so far indicates that *M. rheocharis* is a clear water species. *Mimagoniates microlepis* occurs rarely, if ever, in black acid waters and all our collections of this species came from clear somewhat acid waters. However, these two species apparently are separated (allotopic) at least in some places but we have no information about possible ecological factors preventing syntopy. Furthermore, they have been taken together (syntopic) in two localities, rio Faxinalzinho at Mãe dos Homens, Praia Grande, Santa Catarina, (MZUSP 40278, MCP 13616 and USNM 279878, all *M. rheocharis,* and MCP 13766, *M. microlepis*) and arroio Água Parada, tributary of the rio Maquiné Município de Osório, Rio Grande do Sul, (MCP 13613), *M. rheocharis* and MCP 13625, *M. microlepis*). Thus, in this case black acid waters may have played no role in their speciation although such waters could have formed a barrier in a vicariance event.

At least one species, *Mimagoniates inequalis,* is found in clear and black water streams. This species is often taken in relatively small clear water tributary streams (for example the arroio Paradiso, rio Caí drainage, Rio Grande do Sul, MZUSP 19942, USNM 254275), and we have taken it a few times in small blackwater streams (for example the banhado do Tigre south of Taim, Rio Grande do Sul USNM 254270). The greater adaptability of this species could more easily allow it to introgress with species of more limited ecological tolerance and we have some reason to believe that it may be involved or may have been involved in the past with introgression with either *M. rheocharis* and/or *M. microlepis.* See the Discussion above under *M. rheocharis.*

In another example, the distribution of *M. lateralis,* although geographically completely within (sympatric) that of *M. microlepis,* appears ecologically distinct and therefore allotopic. *Mimagoniates lateralis* appears completely confined to acid black waters and we have never taken *M. lateralis* and *M. microlepis* together even when their respective habitats are contingent. A species such as *M. lateralis* would thus seemingly have limited chances for introgression and we have not found any evidence for this in the populations we have examined. Whatever the ecological adaptations of the various species of *Mimagoniates,* the data indicate that at least broad geographical sympatry occurs in some cases, making the probability of dispersion subsequent to speciation high and producing a possibility of introgression.

Restrictive ecological adaptations, often based on climate, geomorphology and the associated biota, affect speciation in fishes through vicariance, dispersion and/or introgression in very complex ways. We suggest that the species of the Glandulocaudini have been subject to such complexities and that their biogeographical history will not soon be clarified in any detail.

Resumo

Mimagoniates sylvicola e *Mimagoniates rheocharis,* duas espécies de caracídeos brasileiros da tribo Glandulocaudini, subfamília Glandulocaudinae, são descritas como novas. A primeira foi coletada no sul da Bahia, em riachos costeiros de água escura situados ao norte de Cumuruxatiba e em um pequeno tributário do rio Camurugi, perto de Porto Seguro. A segunda é originária de riachos costeiros do sul de Santa Catarina e norte do Rio Grande do Sul. Admite-se que *M. sylvicola* pertence a uma tricotomia não resolvida juntamente com uma linhagem filogenética constituída por *Mimagoniates microlepis* e *M. rheocharis. Mimagoniates lateralis,* conhecida de riachos costeiros de água escura da Costa Atlântica desde as proximidades de Santos, São Paulo até pelo menos próximo de Joinvile, Santa Catarina, ao sul, é morfologicamente mais semelhante a *M. sylvicola.* Estas duas espécies se diferenciam por vários caracteres mencionados na diagnose de *M. sylvicola* e resumidos em uma nove chave para as espécies de Glandulocaudini.

As relações filogenéticas de *M. rheocharis* são incertas e possivelemente complexas. Possíveis hipóteses alternativas de relações filogenéticas desta espécie são discutidas. Com base na presença de uma bomba de feromônio complexa na caudal que representa uma condição derivada e especialmente de espinhos nos raios principais da caudal 10 e 11 distalmente ao complexo de bombeamento de feromônio tanto em *M. rheocharis* como em *M. microlepis,* sugere-se que a primeira seja espécie-irmã da segunda, que distribui-se nos riachos costeiros desde o sul da Bahia até o nordeste do Rio Grande do Sul. *Mimagoniates microlepis* ocorre também na parte alta do rio Iguaçu que drena para oeste, no Paraná. Esta condição de relacionamento filogenético de *M. rheocharis* parece ser a hipótese mais parcimoniosa, mas esta espécie tem a forma do corpo, algumas contagens e proporções corporais e o padrão de colorido pelo menos em exemplares conservados, semelhantes a *M. inequalis.* Também possui alguns caracteres sexuais secundários intermediários entre *M. inequalis* e *M. microlepis.* Assim, não está excluída a possibilidade de *M. rheocharis* ter-se originado de ancestrais de *M. inequalis* e *M. microlepis* por introgressão ou ela pode ser uma espécie-irmã de *M. microlepis* atualmente recebendo fluxo gênico por introgressão com *M. inequalis.* Também é discutida a possibilidade de relacionamento ao nível de espécies-irmãs entre *M. rheocharis* e *M. inequalis,* esta última ocorrendo em riachos costeiros no nordeste do Uruguai e em quase toda a região costeira do Rio Grande do Sul onde ela ocupa uma área adjacente ao limite sul da distribuição de *M. rheocharis* no nordeste do Rio Grande do Sul. Outras hipóteses de relacionamento são apresentadas e algumas discutidas simplesemente para mostrar a natureza possivelmente muito complexa das relações filogenéticas de *M. rhoecharis. Mimagoniates rheocharis* distinguese de *M. microlepis* e *M. inequalis* por características apresentadas na chave e na diagnose de *M. rheocharis.*

As relações filagenéticas e biogeografias filagenéticas das novas espécies são reavaliadas a luz de novos dados e então comparadas com as considerações feitas previamente em um estudo de biogeografia filogenética de Glandulocaudini. Dúvidas são levantadas sobre a filogenia das espécies

de Glandulocaudini, mas corroboração de hipóteses alternativas da filogenia dessas espécies depende da análise de novos dados tanto dentro como fora do grupo.

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